Parasitoids lack adult lipid accumulation, despite functioning fatty acid biosynthesis machinery

Bertanne Visser*[1], Cécile Le Lann*[2], Caroline M. Nieberding[3], Mark Lammers[4], Daniel A. Hahn[5], Thomas Enriquez[1], Mathilde Scheifler[1], Jeffrey A. Harvey[6,7] & Jacintha Ellers[7]

*equal contribution

[1] Evolution and Ecophysiology Group, Department of Functional and Evolutionary Entomology, Gembloux Agro-Bio Tech, University of Liège, Gembloux, Belgium

[2] Université de Rennes, CNRS, ECOBIO (écosystèmes, biodiversité, évolution) – UMR 6553, France.

[3] Evolutionary Ecology and Genetics Group, UCLouvain, Belgium.

[4] Institute for Evolution and Biodiversity, University of Münster, Germany.

[5] Department of Entomology and Nematology, The University of Florida, United States of America.

[6] Department of Terrestrial Ecology, Netherlands Institute of Ecology, The Netherlands

[7] Department of Ecological Science, VU University Amsterdam, The Netherlands

Ruther et al [1] evaluated the ability for *de novo* fatty acid synthesis in 13 parasitic wasp species to test a long-standing claim of a general lack of lipogenesis in parasitoid wasps. In the past 25 years, several different research groups have demonstrated that adults of most insect parasitoid species have an atypical metabolic phenotype. Contrary to other insects, adults of most parasitoids do not increase their lipid reserves when fed surplus carbohydrates (i.e., data for 32 species, and an additional 7 studies on previously tested species; Table 1). This lack of adult lipid mass gain has not only been demonstrated in more than 32 parasitoid wasp species, but also in a wider taxonomic range of insects, including parasitoid flies and a parasitoid beetle [2–4] and in comparison with >90 species of non-parasitoid insects. Finding the same atypical metabolic phenotype in evolutionary independent parasitoid lineages is evidence for convergent evolution for deviating lipid dynamics in parasitoids. Visser & Ellers [5] proposed that lack of adult lipid accumulation may be the evolutionary consequence of a parasitoid lifestyle. Parasitoid larvae can assimilate the lipids produced by their host and thus carry over large triglyceride stores from larval feeding into adulthood (i.e., up to 30 to 40% of the parasitoid's dry body weight; [6,7]), which may render *de novo* lipid synthesis from adult feeding either unnecessary or too costly to maintain, leading to loss of the adult lipid accumulation phenotype [8]. Lack of adult lipid accumulation was confirmed not only by gravimetric or colorimetric comparison before and after feeding (48 experiments reported in 28 studies; Table 1), but also using radioactive and stable isotope labelling studies in multiple species [7,9–11] (Table 1). Because lack of lipid accumulation prevents adult parasitoids from replenishing ebbing lipid reserves, it can lead to significant constraints on energy allocation toward key adult functions, such as maintenance, dispersal, and reproduction [12]. This thus poses a conundrum as to why parasitoids do not increase their lipid reserves as adults and what the underlying genetic and physiological mechanisms are.

This conundrum, however, is not per se what is addressed in Ruther et al's paper [1]. Rather, their report calls for a re-evaluation of the use of the term lack of lipogenesis for the observed phenotypes. Observing lack of lipid accumulation cannot be taken as proof for absence of fatty acid or triglyceride synthesis in adults, because the net increase in lipid reserves hinges on the rate at which lipids are metabolized. This was made very explicit in some early papers (e.g. see the 3rd paragraph of discussion in [9]; and the 2nd paragraph of the discussion in [2];[10]), but should have received more attention during the further course of this research. Moreover, in hindsight, using the term lipogenesis has been a poor choice, because lipogenesis consists of two equally important parts: first, the conversion of glucose or other substrates into fatty acids, and second subsequent biosynthesis of triglycerides [13]. The distinction between these two processes and the accumulation of triglycerides is vitally important in biology, and in previous publications, including our own, the distinction should have been made more explicit.

Ruther et al [1] contribute to this discussion by showing that it is not the lack of ability for fatty acid synthesis that underlies the lack of adult lipid accumulation in parasitoids. They find incorporation of 13C in fatty acids of adult parasitoids that were fed 13C-glucose in 13 parasitoid species, thus showing that parasitoid wasps possess and use the enzymatic machinery to convert glucose into fatty acids. However, in *Nasonia vitripennis,* in which triglyceride synthesis was also investigated, no lipid accumulation was found (replicating earlier findings [10,14]). Instead, their lipid content dramatically and significantly decreased between emergence and 4 days of age, despite feeding on sugar *ad libitum* (see Figure 3a in Ruther et al [1]). Low synthesis of fatty acids is consistent with studies showing that the fatty acid synthase (*fas*) gene is intact in several parasitoid species [7,10,15,16], and that its multiple paralogs are constitutively expressed [10,17–19]. The enzymatic machinery underlying fatty acid synthesis can be involved in other functions than lipid storage, such as the production of cuticular hydrocarbons [20] or pheromones [18]. Echoing earlier studies [7,10,17–19], Ruther et al [1] suggest that *fas* plays a functional role in several aspects of the parasitoid's biology and that the proposed "loss of lipogenesis" comes about via evolutionary changes in transcriptional regulation of lipid synthesis rather than dysfunctionality of the lipogenic machinery. These above findings have led Ruther et al, and other authors, to question whether the phrase, 'lack of lipogenesis' is appropriate [1,18], or if lack of adult lipid synthesis should be considered a form of plasticity [7].

Given the accumulated evidence, we agree that the term 'lack of lipogenesis' should no longer be used in the scientific literature. Instead, we propose to use the more accurate terms 'lack of adult lipid accumulation' and 'fatty acid biosynthesis' to refer to separate and specific processes. The term 'lipid accumulation' is widely used to describe the process of bulk synthesis and storage of triglycerides across a broad range of taxa (e.g., [21–27]). In contrast, the term 'fatty acid biosynthesis' more narrowly defines and denotes the conversion of acetyl Coenzyme

A and malonyl-CoA into palmitic acid. We suggest that a clear distinction between these terms will resolve the misunderstanding about terminology and avoid misleading conclusions when the work is cited (e.g., that adult parasitoids in general can replenish ebbing lipid resources through substantial lipid accumulation [28]). Moreover, it will allow researchers from chemical, ecological and evolutionary backgrounds to unite forces in revealing the mechanisms by which parasitoids do not accumulate substantial lipid reserves as adults and understand the downstream consequences of this lack of lipid accumulation for their life histories. When addressing these questions, both methodologies (gravimetry/colorimetry and isotope labelling) should be used concomitantly to understand how they relate to each other and whether estimated rates of fatty acid synthesis could be interpreted as a good estimate of total triglyceride accumulation. Furthermore, to show that fatty acid synthesis is occurring, it is crucial not only to measure the incorporation levels of tracers into fatty acids in different parasitoid species, but also to include a positive control of incorporation into an insect with typical lipid accumulation (as in [10,11]), so that the relative magnitudes of accumulation can be assessed. For example, Ruther et al [1] found an incorporation rate between 0 and 5% into palmitic acid from 13C-glucose fed to adults (Table 1 in Ruther et al [1]), yet an insect with typical lipid accumulation, e.g., *Drosophila melanogaster*, has a much higher incorporation of stable isotopes, more than 37%, compared to a parasitoid that lacks adult lipid accumulation, e.g., *Eupelmus vuilletti* with only 1% stable isotope incorporation [11].

More than 25 years after the first discovery of lack of adult lipid accumulation in a parasitoid species [29], the question still stands - why did atypically low lipid accumulation evolve in most adult parasitoids and how can parasitoids cope with such low amounts of newly synthesized lipids in adulthood? What we know is that when insufficient lipid amounts are carried over into adulthood from the host, for example in hyperparasitoids (containing 4-8% lipids at emergence; [2,11]), or when development occurs on very lean hosts [7], *de novo* fatty acid synthesis and lipid accumulation can occur in significant quantities in adult parasitoids that consume excess carbohydrates. Moreover, there appears to be genetic variation in how much fatty acids are synthesized, as well as how much lipids are accumulated by adults among wasp lines [7]. Future studies with a range of different parasitoid species should take into account variation in host lipid content, parasitoid genotype, the microbiome [30,31], and plasticity of adult lipid accumulation. Another way to increase our understanding of the mechanisms underlying lack of lipid accumulation is to use inhibitors for key enzymes in the lipid synthesis pathway (e.g., [32]), or manipulate expression of the underlying genes using RNA interference (e.g., [21] or CRISPR-Cas9 [33]. In agreement with Ruther et al [1], we believe that mass spectrometry techniques can play a critical role in understanding the lack of lipid accumulation in parasitoids.

In conclusion, we urge that future work uses more precise definitions for lipid accumulation, as well as the process of fatty acid biosynthesis. We hope that the unambiguous terminology proposed here will help avoid semantic discussion among research groups and unite researchers trying to understand the biological relevance of the lack of adult lipid accumulation in parasitoids. Combining chemistry, ecology, and evolution into a truly interdisciplinary and integrative approach is what we now need for understanding the dynamics of lipid accumulation in parasitoids, and ultimately the downstream life history consequences of accumulating stored nutrients, or not, from adult dietary intake.

Table 1: List of hymenopteran parasitoid species for which studies have looked at lipid accumulation, gene transcription (of genes involved in fatty acid synthesis) and/or fatty acid synthesis. “Yes” refers to an increase in accumulated lipids, gene transcripts or fatty acids; “no” refers to similar (gene transcription, fatty acid synthesis) or lower amounts (adult lipid accumulation).

Species	Lipid accumulation	Gene transcription	Fatty acid synthesis	Reference
Bulk lipid extraction methods (gravimetry or colorimetry)				
Acrolyta nens	yes	-	-	[2]
Apanteles aristoteliae	no	-	-	[34]
Aphelinus abdominalis	no	-	-	[2]
Aphidius ervi	no	-	-	[2]
Aphidius rhopalosiphi	no	-	-	[2,35]
Aphidius picipes (=avenae)	no	-	-	[2,35]
Asobara tabida	no	-	-	[2,29,36]
Bracon hebetor	no	-	-	[37,38]
Cotesia glomerata	no	-	-	[2]
Cotesia rubecula	no	-	-	[2]
Diadegma insulare	no	-	-	[39]
Diglyphus isaea	no	-	-	[40]
Gelis agilis	yes	-	-	[2]
Goniozus nephantidis	no	-	-	[2]

Goniozus legneri	no	-	-	[2]
Leptopilina boulardi	no	-	-	[2]
Leptopilina boulardi	yes + no	-	-	[41]
Leptopilina heterotoma	no	-	-	[6,42]
Leptopilina heterotoma	yes	-	-	[2]
Leptopilina heterotoma	yes + no	-	-	[36]
Leptopilina heterotoma	yes + no	-	yes + no	[7]
Lysibia nana	yes	-	-	[2]
Macrocentrus grandii	no	-	-	[43]
Microplitis mediator	no	-	-	[44]
Nasonia vitripennis	no	no	no	[10]
Nasonia vitripennis	no	-	yes	[1]
Nasonia vitripennis	no	-	-	[45]
Orthopelma mediator	no	-	-	[2]
Orthopelma mediator	no	-	-	[46]
Pachycrepoideus vindemmiae	no	-	-	[2]
Pimpla turionellae	no	-	-	[47]
Pteromalus bedeguaris	no	-	-	[46]
Pteromalus puparum	yes	-	-	[2]
Spalangia erythromera	no	-	-	[2]
Spalangia cameroni	no	-	-	[48]
Tachinaephagus zealandicus	no	-	-	[49]
Trichopria drosophilae	no	-	-	[2]
Venturia canescens	no	-	-	[50,51]
Neochrysocharis formosa	no	-	-	[52]
Meteorus pulchricornis	no	-	-	[53]
Meteorus pulchricornis	no	yes	-	[54]
Gene transcription studies				
Nasonia vitripennis	no	no	no	[10]
Nasonia vitripennis	-	no	-	[17]
Meteorus pulchricornis	no	yes	-	[54]
Isotope tracing				
Anisopteromalus calandrae	-	-	yes	[1]
Asobara tabida	-	-	yes	[1]
Baryscapus tineivorus	-	-	yes	[1]
Cephalonomia tarsalis	-	-	yes	[1]
Dibrachys cavus	-	-	yes	[1]
Eupelmus vuilletti	-	-	no	[9]
Eupelmus vuilletti	-	-	no	[11]

Exoristobia phillippinensis	-	-	yes	[1]
Gelis agilis	-	-	yes	[11]
Gelis aereator	-	-	yes	[11]
Habrobracon hebtor	-	-	yes	[1]
Lariophagus distinguendus	-	-	yes	[1]
Leptopilina heterotoma	yes + no	-	yes + no	[7]
Leptopilina heterotoma	-	-	yes	[1]
Muscidifurax raptorellus	-	-	yes	[1]
Muscidifurax uniraptor	-	-	yes	[1]
Nasonia vitripennis	no	no	no	[10]
Nasonia vitripennis	-	-	yes	[18]
Nasonia vitripennis	no	-	yes	[1]
Nasonia giraulti	-	-	yes	[18]
Nasonia longicornis	-	-	yes	[18]
Tachinaephagus zealandicus	-	-	yes	[1]
Trichogramma evanescens	-	-	yes	[1]
Urolepis rufipes	-	-	yes	[1]

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