

NEV Dissertatieprijs 2012

The evolutionary loss of lipogenesis in parasitoids

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KEY WORDS

Biological control, genomics, Hymenoptera, lipid synthesis, longevity

Entomologische Berichten 75 (3): 97-104

When considering evolutionary change, we tend to think about the acquisition of novel traits, even though trait loss is also very important for evolution. In the 1990's numerous scientists found that parasitic wasps did not synthesize lipids. This finding was remarkable, because lipids are essential nutrients and lipogenesis is a conserved trait across animal species. The hypothesis was formulated that lipogenesis was lost as a consequence of the parasitoid lifestyle. Using a comparative approach this hypothesis was tested, indeed revealing that lipid synthesis was lost at least three times independently in parasitic wasps, parasitic beetles and parasitic flies. The loss of lipogenesis thus evolved in association with the parasitoid lifestyle in insects. A closer look into the genomic and physiological mechanisms underlying lack of lipogenesis further revealed that a transcriptional response to feeding was lacking for the key gene and enzyme involved in lipid synthesis, i.e. fatty acid synthesis. The loss of lipogenesis in parasitoids is exceptional and provides an excellent example of compensated trait loss, where a symbiotic partner provides a phenotypic function that is consequently lost in the receiving organism. This phenomenon is expected to be much more common than currently appreciated and might have far-reaching consequences for species dynamics and interactions.

Evolutionary change

A major focus in evolutionary biology has intuitively been on the origin of novel traits, i.e. why and how new adaptations increase reproductive success following environmental change. Such novelties include the evolution of helmets in treehoppers that provide better camouflage, thereby increasing survival and reproduction (Prud'homme et al. 2011). Another example can be found in beetles, where males of some species have evolved extensive horns to fight off potential competitors to increase their chances of securing a mate and thereby reproductive success (Emlen et al. 2007). In both these cases, selection has favored individuals bearing novel traits allowing them to cope better with environmental challenges.

Selection can favor the acquisition of new traits, but evolutionary change can also follow a different direction. Under certain circumstances it can be beneficial to reduce trait expression or to lose a trait completely, for instance when maintaining the trait bears energetic costs. Here, negative selection on the trait results in higher fitness for individuals without the trait. Traits can be lost when selection on a trait is intense, but trait loss can also result when selection is absent, i.e. trait expression is neutral when maintaining the trait is neither costly nor beneficial. Traits are thus lost when they remain unused. The loss of wings in flightless birds and insects provide clear examples of traits that are lost because they are redundant or too costly to maintain (Fong et al. 1995, Porter & Crandall 2003). While the origin of novel traits is an appealing area of research, the importance of trait loss in shaping trait dynamics must not be overlooked. The loss of a trait can considerably alter

the evolutionary potential of species and trait loss can play an important role in shaping the evolutionary trajectories of lineages.

The lack of lipogenesis in parasitic wasps

Trait loss can most easily be deduced when organisms have lost large morphological structures, such as wings or limbs. For other traits, such as those involved in physiology or biochemical processes, the loss of a trait may not be as evident and typically requires more refined measurements. Starting with observations in the 1990s, numerous researchers found that parasitic wasps (Hymenoptera) showed an atypical metabolic response to feeding (Ellers 1996, Eijs et al. 1998, Olson et al. 2000, Rivero & West 2002, Giron & Casas 2003). Physiological measurements of fat content revealed that parasitic wasps did not convert sugars and other carbohydrates into fat, despite the fact that they did consume sugars and carbohydrates in these feeding experiments (figure 1). This is in contrast with the typical response to feeding found in most other animal species, where excess nutrients obtained through feeding are immediately stored into their lipid reserves.

The lack of lipid synthesis (or lipogenesis) in parasitic wasps is remarkable, because lipids are essential resources for nearly all animals (Arrese & Soulages 2010). It is, therefore, not surprising that metabolic pathways involved in lipid metabolism are highly conserved in animals (Turkish & Sturley 2009). Lipids are important nutrients due to their exceptionally high energetic value. Lipids contain most energy compared to any other form

NEV-Dissertatieprijs 2012

Tijdens de 24e Nederlandse Entomologendag (Ede, 14 december 2012) is de vijfde NEV-Dissertatieprijs uitgereikt aan Dr. Bertanne Visser, voor haar proefschrift 'Parasitism and the evolutionary loss of lipogenesis', op 25 januari 2012 verdedigd aan de Vrije Universiteit Amsterdam. De prijs bestaat uit een geldbedrag plus een oorkonde en wordt jaarlijks toegekend voor het beste proefschrift op het gebied van de entomologie, verdedigd aan een Nederlandse universiteit in het voorgaande academische jaar (1 september – 31 augustus). Vissers proefschrift beschrijft een studie naar de relatie tussen een parasitaire levensstijl en het verlies van vetaanmaak bij sluipwespen. De commissie prijst de integratieve en multidisciplinaire benadering van het onderzoek in dit proefschrift. Het is onderzoek aan een wetenschappelijk relevant onderwerp en een diversiteit aan parasitaire soorten. Ook zijn er implicaties voor agro-ecosystemen. De schrijfstijl is excellent, en het proefschrift heeft een mooie lay-out. Dit onderzoek heeft ook veel aandacht in de media gekregen.

During the 24th Annual Dutch Entomologists Meeting (Ede, 14 December 2012), the fifth Netherlands Entomological Society (NEV) Dissertation Award was presented to Dr. Bertanne Visser, for her thesis 'Parasitism and the evolutionary loss of lipogenesis', defended on 25 January 2012 at the Free University of Amsterdam. This price comprises a sum of money and a certificate of appreciation, and is awarded for the best doctoral thesis in the field of entomology, defended at a Dutch university in the preceding academic year (1 September – 31 August). Visser's thesis describes a study on the relationship between the parasitic lifestyle and the loss of lipogenesis in parasitoids. The committee especially appreciated the integrative and multidisciplinary approach of the research described in this thesis. The study is scientifically relevant and includes a diversity of parasitic species. There are implications for agro-ecosystems. Visser's writing style is excellent and the layout of the thesis is nice. This study also received a lot of media-attention.



of energy storage and burning stored lipid reserves allows organisms to overcome unfavourable environmental conditions. Harsh conditions include times when food might not be readily available, such as during overwintering. Lipids can further be used to increase longevity and are also important for reproduction, because the eggs of many animals are rich in lipids (Giron & Casas 2003). Lipids can further provide the necessary fuel for intensive activities, for instance during long migratory flights observed in locusts (Mentel *et al.* 2003). But if lipids form such an essential resource for fuelling key functions during life, how can it be possible that a whole group of animals does not seem capable of synthesizing fat?

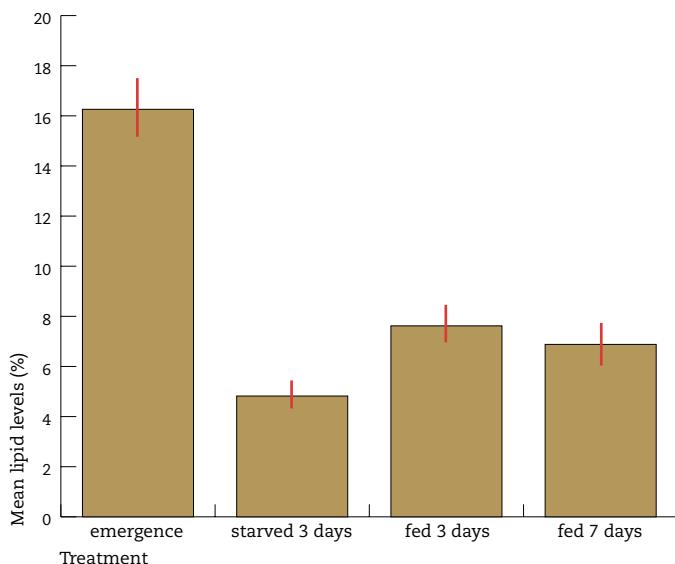
Why the parasitoid life style should lead to loss of lipogenesis

Although at first glance parasitic wasps might seem quite similar to their close relatives, the stinging wasps and bees, parasitic wasps have adopted a rigorously different life style during development (Godfray 1994). Parasitic wasps need to feed on or inside an arthropod host to successfully complete their development (figure 2). They are thus parasitic, but only during development, because the adults are free-living to search for new hosts. Such a lifestyle is characteristic of parasitoids, a collective term that is applicable also to several groups outside of Hymenoptera, such as parasitic beetles and flies. In order for a female's offspring to develop on a host, she needs to subdue her victim, for instance by slowing down or arresting its

development or by repressing the host's immune system. By manipulating the host, a female can assure more favourable environmental conditions for her offspring through the injection of substances along with her egg(s) during oviposition (Rivers & Denlinger 1994, 1995, Nakamatsu & Tanaka 2004). Parasitoids have thus evolved an intricate lifestyle, where larvae develop in close association with their hosts. This lifestyle enables them to take over and use costly nutrients, such as lipids, directly from their host, providing them with an energetic advantage. As a result, lipid synthesis in parasitoid larvae becomes evolutionary neutral or is even selected against, which could result in the evolutionary loss of lipid synthesis.

Putting the ideas to the test

To formally test the hypothesis that lipogenesis has been lost during the course of evolution as a consequence of the parasitoid lifestyle, information on lipogenic ability in more species was required. Moreover, to evaluate whether or not such patterns arose in parallel and irrespective of common ancestry, sampling needed to include groups other than Hymenoptera, such as beetles and flies. Data was first collected by searching the literature for known cases describing lipogenesis in insects. This exhaustive search led to data on lipogenic ability in 70 different species from a wide range of insect orders. An additional 24 insect species were tested for their lipogenic ability (Visser *et al.* 2010), including a parasitoid fly, a parasitoid beetle, a hymenopteran non-parasitoid (sawfly) and 21 parasitic



1. Unlike other insects, lipid levels in adults of the parasitoid *Nasonia vitripennis* do not increase, despite feeding on sugars.

1. In tegenstelling tot andere insecten nemen vettniveaus in de sluipwesp *N. vitripennis* niet toe als ze suikers eten.

hymenopterans. Testing whether or not a species synthesizes lipids is straightforward. Adult females are allowed to feed on sugar during a fixed proportion of their lives. Lipid content is then determined before and after feeding. Lipid levels will increase in species with active lipogenesis, whereas species lacking lipogenesis show decreasing or stable lipid levels (figure 1). Data obtained from the literature and experiments thus yielded information on lipogenic ability for 94 species from all major insect orders.

To find correlations in trait evolution, one needs to resort to comparative methods to take into account common ancestry.

Such a methodology requires knowledge of phylogenetic relationships to trace the evolutionary fate of certain traits. Tracing traits onto a phylogeny enables a better analysis of trait evolution, taking into account only independent evolutionary changes when testing for correlated evolution of traits. In the case of parasitoids, one can determine whether or not the evolution of the parasitoid lifestyle preceded or coincided with the lack of lipogenesis (figure 3).

Parasitism evolved on numerous occasions in insects and the phylogeny that was compiled for testing correlated evolution between parasitism and lack of lipogenesis showed that parasitism arose at least three times (figure 3, Visser et al. 2010). In all of these cases, species composing these parasitic clades also lacked lipogenesis whereas close relatives had the ability to synthesize lipids. Conforming to expectations, phylogenetic analysis indeed showed that the lack of lipogenesis evolved as a consequence of the parasitoid lifestyle. Moreover, lack of lipogenesis had evolved several times in parallel in parasitic wasps, beetles and flies. The evolution of these two traits is thus correlated and has occurred in independent replicated evolutionary events in insects.

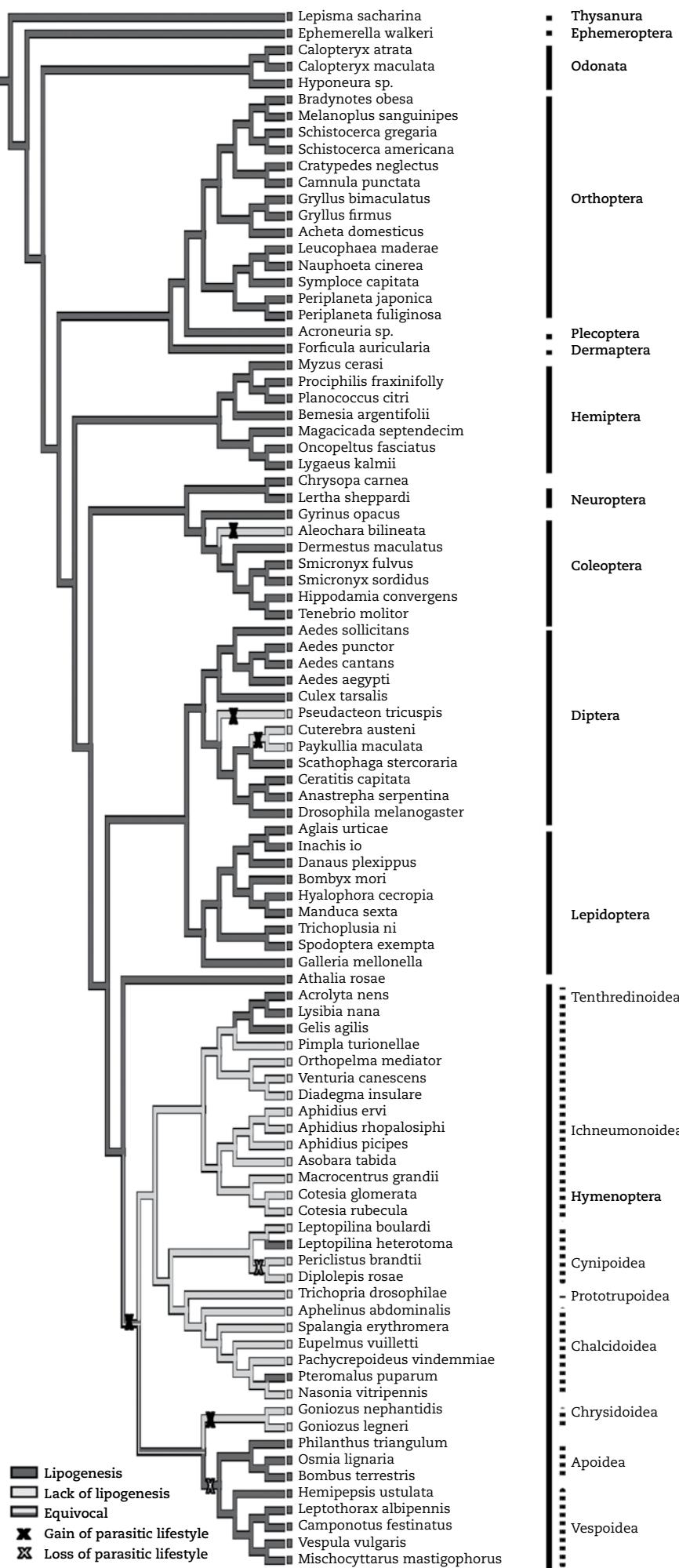
Lipogenesis regained

Remarkably, not all of the hymenopteran parasitoid species that were tested conformed to this pattern. Some parasitic wasp species did synthesize lipids. The phylogeny showed the trait to have re-evolved despite the parasitic larval lifestyle (figure 4). This led to the question as to why only these few species deviated from most other parasitoids by re-evolving lipogenesis. The answer lies in the incredible diversity of parasitic hymenopterans, a group of insects with surprising ingenuity as to the ways in which they exploit their hosts. Among parasitoids, a wide range of traits is related specifically to host exploitation strategies, for instance the induction of host developmental arrest and variation in the number of offspring able to develop on one host. By evaluating the evolutionary



2. The parasitoid *Cotesia glomerata* stings its caterpillar host. The parasitoid larva continues feeding and growing inside its host until it is ready to pupate outside the host's body. After completing its development, the adult is free living to search for hosts or mates. Photo: Hans Smid, www.bugsinthepicture.com

2. De sluipwesp *Cotesia glomerata* stekt een rups van het grote koolwitje. De larve van de sluipwesp vreet en groeit in het lichaam van de gastheer tot hij klaar is om te verpoppen buiten de rups. De volwassen sluipwesp is vrijlevend en zoekt naar gastheren of partners.



3. Lipid synthesis was lost at least three times (light gray branches) following the evolution of the parasitoid life style (x) in insects. Dark gray branches indicate taxons with lipid synthesis.

3. Vetaanmaak is minstens drie keer verloren gegaan (lichtgrijze takken) volgend op de evolutie van de parasitoïde levensstijl (x) in insecten. Donkergrijze takken geven taxons aan waar vetaanmaak wel aanwezig is.



a



b



c

4. Lipid synthesis was regained on three separate occasions in parasitic wasps, including the wasps (a) *Gelis agilis* (Fabricius), (b) *Acrolyta nens* (Hartig) and (c) *Lysibia nana* (Gravenhorst) (Hymenoptera: Ichneumonidae). Photos: Tibor Bukovinszky, www.bugsinthepicture.com

4. Vetaanmaak is in drie verschillende gevallen weer ontstaan in sluipwespen, zoals *Gelis agilis* (Fabricius) (a), *Acrolyta nens* (Hartig) (b) en *Lysibia nana* (Gravenhorst) (c) (Hymenoptera: Ichneumonidae).

routes taken by parasitoid-specific traits and lipogenesis, we found only one trait was correlated with the re-gain of lipogenesis: Host range. Parasitoids can attack different numbers of host species and whilst some species are highly specialized and lay eggs only on one type of host, others can exploit over fifty different host species. Generalist parasitoids thus re-evolved lipogenesis, probably due to difficulties associated with manipulating numerous host species and the variability in lipid quantity that can be acquired from different types of host (figure 4, Visser et al. 2010).

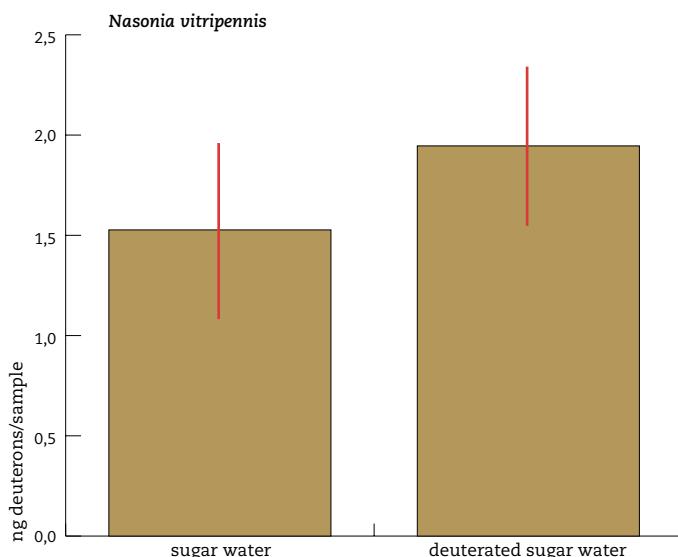
Mechanisms and life-history consequences

Lipid synthesis was lost repeatedly in insects with a parasitoid lifestyle, but what is the mechanism behind the loss of lipogenesis? To find that out it was necessary to look more closely at the biochemical pathways that underlie sugar and lipid metabolism. Lipid reserves help animals overcome challenging environmental conditions, and fatty acids are essential molecules needed for the production of storage lipids. It can, therefore, be expected that compromised functioning of the fatty acid synthesis pathway underlies the loss of lipogenesis (Visser et al. 2012). The enzyme fatty acid synthase is the only enzyme responsible for the production of fatty acids, and it is critical to evaluate whether or not this specific enzyme is functioning properly in parasitoids. By feeding insects stable isotopes, it is possible to track the incorporation of specific atoms into the fatty acid fraction using mass spectrometry. Indeed, the honeybee

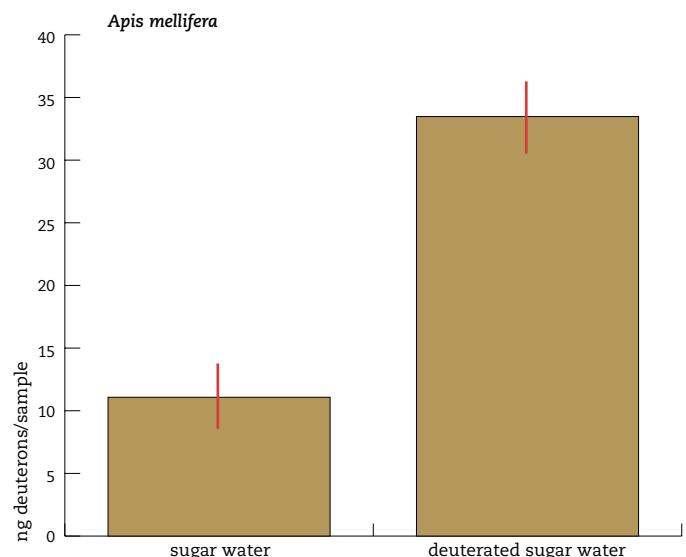
Apis mellifera Linnaeus, a species capable of synthesizing lipids, readily incorporates the isotopes into its fatty acid fraction (figure 5, Piek 1964, Toth et al. 2005, Ament et al. 2011). Parasitoids, however, do not incorporate the isotopes and the enzyme fatty acid synthase does not seem to function properly, explaining why adult parasitoids do not produce fatty acids (figure 5).

Underlying enzyme formation is gene transcription. In response to certain stimuli, specific genes are targeted and up regulated, leading to an increase in transcript numbers that are subsequently translated into enzymes. Transcript abundance can thus be used as an indirect predictor of enzyme levels. To learn more about the response of key genes involved in sugar and lipid metabolism, gene transcription patterns were quantified in the parasitoid *Nasonia vitripennis* (Walker), an excellent model system for genomic analysis due to the recent completion of its full genome sequence (Werren et al. 2010). 28 key genes involved in nutrient metabolism were targeted and the transcriptional response analyzed in female parasitoids following sugar feeding and starvation (Visser et al. 2012). Starvation led to the up regulation of genes involved in sugar breakdown, a typical metabolic response required to increase sugar levels from within the body. In contrast, the gene fatty acid synthase (*fas*) did not respond to dietary conditions. A lacking responsiveness of this gene opposes findings in insects that do synthesize lipids, because *fas* is typically highly up regulated in response to sugar feeding (Zinke et al. 2002). Lack of lipogenesis in parasitoids thus results from the lack of a transcriptional response of *fas*.

a



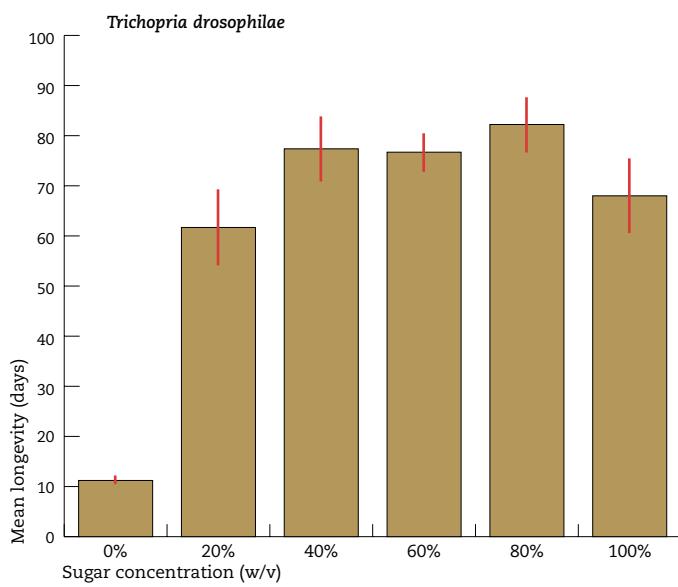
b



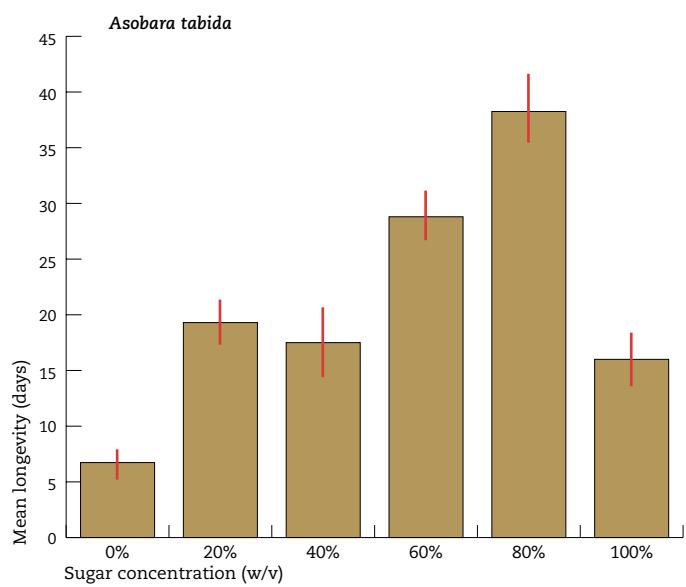
5. (a) The parasitoid *Nasonia vitripennis* does not incorporate stable isotopes (deuterons) into its fatty acid fraction (palmitate). (b) The honey bee *Apis mellifera* readily uses stable isotopes for the synthesis of fatty acids ($P < 0.001$).

5. (a) De sluipwesp *Nasonia vitripennis* neemt geen stabiele isotopen (deuteronen) op in de vetzuurfractie (palmitaat). (b) De honingbij *Apis mellifera* gebruikt wel stabiele isotopen voor de aanmaak van vetzuren ($P < 0.001$).

a



b



6. The parasitoid wasps (a) *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae) and (b) *Asobara tabida* (Nees) (Hymenoptera: Braconidae) do not benefit from a high-caloric diet, i.e. longevity is lower at higher sugar concentrations.

6. De sluipwespen (a) *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae) en (b) *Asobara tabida* (Nees) (Hymenoptera: Braconidae) hebben geen voordeel van een dieet met veel calorieën, de levensduur is lager bij hogere suikerconcentraties.

While lacking lipid synthesis can benefit larvae by reducing costs, for adults the advantages are less obvious, especially since reproduction occurs only in the free-living adult stage. Not being able to synthesize lipids could severely constrain investment into eggs, but the acquisition of nutrients other than lipids through feeding might be an important strategy that allows parasitoids to optimize their reproductive output. A way to increase energy levels is by consuming calorie-rich substrates, such as nectar or honeydew. Contrary to expectations, however, parasitoids do not seem to benefit from a sugar- and calorie-rich diet. When the parasitoids, *Asobara tabida* (Hymenoptera: Braconidae) and *Trichopria drosophilae*

(Hymenoptera: Diapriidae) were fed sugar diets of varying concentrations, the highest sugar concentration reduced rather than extended longevity (figure 6, Ellers et al. 2011). A similar result was found when the parasitoid *Cotesia glomerata* (Linnaeus) (Hymenoptera: Braconidae) was fed a diet rich in lipids. Although females were able to attain higher income lipid levels by feeding on a sugar source enriched with lipids, their longevity was reduced (Visser & Ellers 2012). Parasitoids are thus not only constrained by the lipid levels obtained as larvae, but also by resources acquired as adults, since energy-rich nutrients obtained through feeding negatively affect key life history traits.

The loss of lipogenesis through symbiosis

Lipogenesis was lost repeatedly as a consequence of the parasitoid lifestyle and evolved in parallel in parasitoid wasps, flies and beetles. Underlying the loss of lipogenesis is the lacking response of the enzyme and gene encoding fatty acid synthase, an important player in the lipid biosynthetic pathway. The lack of lipogenesis illustrates how unused or costly traits can lead to evolutionary trait loss, but also exemplifies the extent to which some insects depend on an interaction partner for essential resources or functions. This new concept, termed compensated trait loss, pertains to organisms that lose essential functions when these are provided by a symbiotic partner (Visser et al. 2010, Ellers et al. 2012). Compensated loss of behavioral, morphological and physiological traits is common in nature and occurs in organisms ranging from bacteria to humans. Moreover, compensated trait loss increases the dependence of organisms on their interaction partner. Sudden environmental changes, such as those anticipated in the face of global climate change, might thus force interacting

partners to split up. Consequently, organisms will be forced to face environmental challenges without their interaction partner, which can have serious and potentially irreparable fitness consequences.

Acknowledgements

I would like to thank my promotor, Jacintha Ellers, co-authors, Jacques van Alphen, Frank den Blanken, Coby van Dooremalen, Daniel Hahn, Jeffrey Harvey, Cécile Le Lann, Janine Mariën, Dick Roelofs, Bas Ruhé, Peter Teal, Alba Vázquez Ruiz, and the section Animal Ecology of the VU University Amsterdam. This research was funded by the Netherlands Organisation for Scientific Research (NWO), ALW-grant no. 816-01-013. A digital copy of my thesis is available at <http://dare.ubvu.vu.nl/handle/1871/32688> and more information about my research is available at www.bertannevisser.nl.

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Accepted: 1 April 2015

Samenvatting

Het evolutionaire verlies van vetaanmaak bij parasitoïden

Veel onderzoek richt zich op het ontstaan van nieuwe kenmerken, maar het verlies van eigenschappen speelt ook een belangrijke rol in evolutie. Het verlies van eigenschappen kan gebeuren als een eigenschap neutraal is of als het selectief voordelig is een kenmerk te verliezen, bijvoorbeeld omdat behoud van een eigenschap kosten met zich meebrengt. In de jaren 1990 werd bekend dat sommige sluipwespen niet het vermogen hebben om vetten aan te maken. Dit is opmerkelijk omdat vetten essentiële stoffen zijn en alle dieren suikers kunnen opslaan in de vorm van vetten. In tegenstelling tot de meeste andere insecten hebben sluipwespen een levensstijl waarbij de larven parasitair zijn en zich voeden met andere geleedpotigen, terwijl de volwassenen vrij levend zijn om nieuwe gastheren te zoeken. Het bleek dat alle insecten met een gebrekkige vetaanmaak een parasitaire levensstijl hadden aangenomen. Dit leidde tot de hypothese dat het evolutionaire verlies van vetaanmaak een gevolg is van de parasitaire levensstijl. Een fylogenetische analyse wees inderdaad uit dat vetaanmaak alleen verloren was gegaan in parasitaire wespen, kevers en vliegen. Er is sprake van parallelle en gecorreleerde evolutie tussen parasitisme en het verlies van vetaanmaak. Om meer inzicht te krijgen in het mechanisme achter het verlies van vetaanmaak werd verder gekeken naar genexpressie van 28 belangrijke genen betrokken bij suiker en- vetmetabolisme in de sluipwesp *Nasonia vitripennis*. De gentranscriptie in sluipwespen wijkt sterk af van dat in andere insecten, in het bijzonder fatty acid synthase, dat niet wordt opgereguleerd na het voeden met suikers. Met behulp van stabiele isotopen werd verder aangetoond dat het enzym voor de vetzuursynthese geen vetzuren maakt. Het verlies van vetaanmaak in parasitaire insecten is een uitstekend voorbeeld van gecompenseerd functieverlies, waarbij een partnersoort in een fenotypische functie voorziet, met een verlies van functie in de ontvangende partner tot gevolg. Dit fenomeen is naar verwachting veel voorkomend en kan belangrijke gevolgen hebben voor de dynamiek en interacties tussen soorten.



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