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Review

Resource allocation and compensation during development in holometabolous insects

David Nestel [a,*], Nikos T. Papadopoulos [b], Carlos Pascacio-Villafán [c], Nicoletta Righini [c], Alma R. Altuzar-Molina [c], Martín Aluja [c]

[a] Institute of Plant Protection, Dept. of Entomology, ARO, The Volcani Ctr., Beit Dagan 50250, Israel
[b] Laboratory of Entomology and Agricultural Zoology, Dept. of Agriculture Crop Production and Rural Environment, University of Thessaly, N. Ionia, Volos, Greece
[c] Instituto de Ecología, A.C., Clúster Científico y Tecnológico BioMimic®, Red de Manejo Biorracional de Plagas y Vectores, 91070 Xalapa, Veracruz, Mexico

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ABSTRACT

We provide an extensive review on current knowledge and future research paths on the topic of resource allocation and compensation during development in holometabolous insects, emphasizing the role of resource management during development, and how compensatory mechanisms may be acting to remediate nutritional deficiencies carried over from earlier stages of development. We first review resource allocation in "open" and "closed" developmental stages and then move on to the topic of modelling resource allocation and its trade-offs. In doing so, we review novel methodological developments such as response-surface methods and mixture experiments as well as nutritional geometry. We also dwell on the fascinating topic of compensatory physiology and behavior. We finish by discussing future research paths, among them the emerging field of nutrigenomics and gut microbiome, which will shed light into the yet poorly understood role of the symbiotic microbiota in nutrient compensation or assimilation.

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* Corresponding author.
E-mail address: nestel@agri.gov.il (D. Nestel).

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Nutritional ecology lies at the heart of life-history expression and evolution

[Boggs (2009)]

1. Introduction

Nutrient and energy allocation for specific life functions across the immature and adult stages of holometabolous insects is subordinated to genetic codes and shaped by the environment. Insects exhibit a variety of metabolic regulation mechanisms between feeding (i.e., larvae and adults) and non-feeding stages (i.e., eggs, pupae and diapausing individuals). Resource acquisition and allocation during these transitions is expected to affect all developmental stages and ultimately fitness.

Insights obtained from past studies on resource allocation were summarized by Boggs (2009) as follows: (1) there is a requirement for resource congruence and specific nutrient proportions for the optimal metabolic allocation of resources in the organism, (2) allocation processes and nutrient limitations are associated with the timing of resource acquisition, (3) physiological trade-offs may also occur across developmental stages, and (4) the pattern of resource allocation and the expression of trade-offs respond to environmental stress, with considerable variability across organisms and species. While some aspects of resource allocation have been more extensively investigated, the mechanisms and expression of resource compensation, especially at the inter-stadia level, are still poorly understood. Here, we present recent advances in the understanding of resource allocation of holometabolous insects, emphasizing the role of resource management and allocation during development, and how compensatory mechanisms may be acting to remediate nutritional deficiencies carried over from earlier stages of development. We also advance some ideas on useful experimental approaches to explore resource management and compensation during development.

2. Resource allocation and development in holometabolous insects: managing resources in "open and "closed developmental stages

Holometabolous insects go through several developmental phases, each having a different function in their life-history. Maternal resources are metabolized for the production of offspring during embryogenesis, whereas the larval stage is a period of active acquisition of nutrients from the environment that are incorporated into body mass (Arrese and Soulages, 2010). During the pupal stage, the individual undergoes a radical transformation and reorganization of the body, using exclusively the energetic resources incorporated during the larval stage (Denlinger and Zdarek, 1994). The "transformed" individual that emerges as an adult from the puparium, uses and manages the remaining energetic metabolites carried over from the larval stage but, in general, is also able to actively acquire resources from the environment to complete sexual development and reproduce (Jervis et al., 2008).

Energy flow between the environment and the insect can be relatively large and bidirectional, such as when the organism is in a feeding stage, or relatively small and unidirectional, as during non-feeding stages (Downer, 1981, Fig. 1). This relationship can be described as "open", for feeding stages, and "closed" for non-feeding stages (Boggs, 2009).

2.1. Resource allocation in "open" developmental stages

2.1.1. The larval stage

Larvae of holometabolous insects go through several instars, each allowing the individual to increase in size by feeding (Chown and Gaston, 2010). The nutrients and energy acquired in the larval stage are used across the immature and adult stages for the biosynthesis and correct functioning of internal and external structures (Sentinella et al., 2013; Runagall-McNaull et al., 2015). Nutrients are also allocated to storage, providing the basis for the adequate development and growth of the organism and the accumulation of energy reserves in the fat body for subsequent non-feeding stages and for the adult stage (Arrese and Soulages, 2010). As such, we expect that insects will optimize food intake (i.e., the ingestion of a balanced amount and type of nutrients that will maximize survival and fitness), allocating resources for development and for the accumulation of reserves. Tephritid larval feeding behavior on fruit hosts, as an example, has been linked to the optimization of foraging by the developing larvae during the search for the most nutritive sectors within the fruit, where sugar and solutes are at a higher concentration (Yuval and Hendrichs, 2000). Optimization of nutrition at the larval stage of holometabolous insects, however, is highly dependent on the mother's behavior and ability to select appropriate hosts during egg-laying (Papaj and Aluja, 1993; Balagawi et al., 2013).

The actively feeding and developing larvae incorporate metabolic reserves (e.g., lipids, glycogen and storage proteins) (Arrese and Soulages, 2010). The quantity and quality of the larval diet can affect the allocation of resources to different functions. For instance, the sugar and amino acid content of artificial larval diets has been shown to affect the ability of pupating tephritid larvae to accumulate lipid and protein reserves (Nestel et al., 2004; Nestel and Nemny-Lavy, 2007). Direct allocation of resources during larval development to future adult body structures (through the imaginal discs) has also been documented in several holometabolous orders (Shingleton et al., 2007); regulation of the adult body and organ size, including the fat body, will depend on the acquisition of nutritional resources during larval development (Chown and Gaston, 2010).

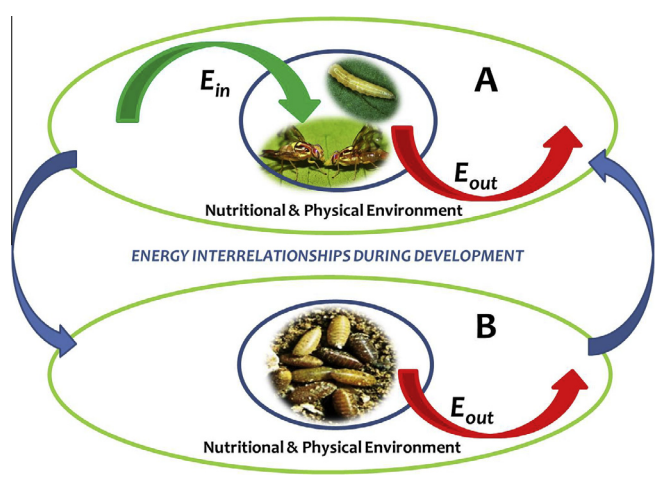

Fig. 1. From an energetic perspective, developmental stages in holometabolous insects comprise stages with: (**A**) **open energy flow** (in larvae and adults), in which energy and nutrients are acquired from food and the physical environment (E_{in}), and energy is used and transformed (E_{out}) during growth and development; and (**B**) relatively **closed energetic stages** (eggs, pupae, and during diapause), in which energy is mainly used for maintenance and metamorphosis. In **open** developmental stages, the flow of energy through the system may be balanced ($E_{in} = E_{out}$), positive ($E_{in} > E_{out}$) or negative ($E_{in} < E_{out}$) (Downer, 1981). In addition, the acquisition of specific food components, such as essential micro and macro-nutrients, may be deficient, affecting not only the development and function of the feeding stage, but also affecting other developmental stages. In the relatively **closed** developmental stages, the organismal system may, in general, be in a negative energetic balance. This interrelationship between open and closed energy systems during the development of holometabolous insects ("Dynamic Energy Budget", DEB), and the ability of evolving stages to compensate for deficiencies, lies at the basis of the organismal fitness.

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