

## The Advantages and Consequences of Holometabolous Development in Insects

Holometabolous development in insects, or holometaboly, can be defined as “*development in which the body form abruptly changes at the pupal moult; complete metamorphosis*” (Gullan PJ & Cranston PS, 2014). It is characterized by a life cycle in which an egg is proceeded by a morphologically reduced larva. Following this, the larva transforms into a predominantly quiescent pupa before developing into a sexually mature adult.

The alternatives to holometaboly in insect orders are ametaboly or hemimetaboly. These can be defined as “*lacking metamorphosis, i.e. with no change in body form during development to the adult, with the immature stages lacking only reproductive structures*” and “*development in which the body form gradually changes at each moult, with wing buds growing larger at each moult; incomplete metamorphosis*” respectively (Gullan PJ & Cranston PS, 2014). Ametabolous species lack a change in appearance due to the absence of wing buds in the adult forms and the continuous moulting to form a new cuticle throughout its life. In hemimetabolous insects, the pronymph will quickly develop into a nymph after hatching in a stage that often goes unnoticed. This nymph partially resembles adult insects but is sexually immature and has wing buds as opposed to fully developed wings (Engel MS, 2015).

In hemimetaboly, the developing wings are visible on the dorsal surface of the nymphs. Species that display this trait are called exopterygotes; this can be defined as development in which “*the wings form progressively in sheaths that lie externally on the dorsal or dorsolateral surface of the body*” (Gullan PJ & Cranston PS, 2014). However, holometabolous species have a pupal stage where the main structural differences between larvae and adults develop. Adult structures arise internally in larvae as undifferentiated cells known as imaginal discs. The term endopterygote can therefore be defined as “*describing development in which the wings form within pockets of the integument, with eversion taking place only at the larval-pupal moult*” (Gullan PJ & Cranston PS, 2014).

Holometaboly has been undoubtedly successful in increasing fitness and reproductive success among insects brought about by a number of advantages to this life cycle. These will be explained in this essay as well as the minor disadvantageous consequences.

### Nutritional Advantages

In holometabolous species, newly hatched insects will take the form of larvae, whereas hemimetabolous insects will hatch to pronymphs and subsequently nymphs. The difference between these two manifestations has been compared with regard to the nutritional advantages that holometaboly brings.

In an experiment, Bernays compared the growth rate, respirometry, consumption and assimilation, and the investment of nutrient in cuticle between two insect species. The species chosen were *Melanoplus sanguinipes*; a hemimetabolous exopterygote acridid, and *Pseudaletia unipuncta*; a holometabolous endopterygote noctuid. The species were at the nymph and larval stage respectively and the experiment was terminated when the adults emerged from pupation (Bernays EA, 1986).

In both species, fourth instar larvae were fed daily with weighed samples of wheat until the fifth stadium where ecdysis took place (the process of casting off a cuticle following moulting/the formation of a new cuticle (*Gullan PJ & Cranston PS, 2014*)). Following this, consumption of food and efficiency of conversion to body mass were measured. The proportion of body weight in the cuticle as well as the proportion of this cuticle lost in the exuviae was calculated (*Bernays EA, 1986*).

The results obtained from Bernay's experiment indicated that growth rates were much higher in the holometabolous *P. unipuncta* at this life stage than they were in hemimetabolous *M. sanguinipes*. Five days into the experiment, Bernay recorded that the insects were of similar mass but the average growth rate for *P. unipuncta* was  $0.7 \pm 0.04$  mg/mg/day but  $0.2 \pm 0.01$  mg/mg/day for *M. sanguinipes*. The average growth rate across the entire experiment was 0.19 mg/mg/day higher for the noctuid than it was for the acridid. The mean consumption rates were more than double in *P. unipuncta* and the efficiency of conversion of this food to biomass was 50% greater. Although a larger proportion of the body mass as a percentage of total production was lost in exuviae (13.9% vs. 10.7%) there is a significant difference between the investment of body mass in the cuticle. 4.2% of *P. unipuncta*'s body mass was cuticle whereas in *M. sanguinipes* the cuticle was 49%. The difference between the two species was therefore clear in which was more efficient at consuming and using the food to create body mass (*Bernays EA, 1986*).

Multiple implications can be taken from the results of this experiment. Bernay's results show that although there are no significant differences in respiration rates between the two species, the growth rate was much greater in *P. unipuncta*. From this it can be drawn that the use of oxygen and energy with regard to growth is much more efficient in holometabolous species at the larval stage where they exist as caterpillars. The average daily values for conversion of food to biomass was 8.5 mg compared to 2.4 mg in the acridid species, thus demonstrating this advanced efficiency. A reason for this increased efficiency may be the lack of a need to produce and/or maintain a large mass of cuticle in their larval form. This means a higher proportion of nutrition can be invested in the production of other biomass that is not regularly shed and reassembled (*Bernays EA, 1986*).

As well as this increased efficiency in conversion of food to biomass, holometabolous species are also able to physically consume much more in the same period of time. This is presumably related to the fact that in this experiment the caterpillar had double the gut capacity than the acridid, a trait that would be seen across many species.

These characteristics of nutritional efficiency and consumption capacity are advantageous for holometabolous species. Compared to hemimetabolous forms, they are able to gain mass at a greater rate such that they can invest a greater amount of biomass into the development of an adult form.

### Separation of Modes of Life

The large morphological distinction between a holometabolous individual during different life stages is an advantageous characteristic in this group. The developmental dissociation between stages exists such that the different morphologies

act as adaptively significant phenotypic traits for a particular mode of life. In short, this means that the forms of insects at different life stages are sufficiently dissimilar such that there is less intraspecific competition between individuals of different ages due to the exploitation of different resources and habitats. This in turn increases population growth (*Yang AS, 2001*). Truman and Riddiford outline this developmental distinction between the different stages in holometaboly. The authors correspond the stages to their equivalent hemimetabolous stages, highlighting the adult and juvenile modularity and specialisation to different lifestyles only present in holometaboly (*Truman JW & Riddiford LM, 1999*).

An example of the specialisation to different niches throughout the life cycle is the feeding stage in larvae. This refers to the adaptations of nutritional efficiency shown in Bernay's experiment. The modularity between the larvae being associated with feeding and adults with reproduction has led to independent evolution of the stages. This results in higher rates of diversification as well as greater adaptation to the niche within a stage (*Yang AS, 2001*). For example, highly specific mouthparts to consume different vascular plants have evolved among the holometabolous larvae to increase the efficiency of consumption. 23 different mouthpart types have been identified in the holometabola compared to just 11 in the hemimetabola, indicating both the high diversity as well as specific adaptation of the structure (*Labandeira CC, 1997*). As well as this, the guts in caterpillar larvae will generally be shorter, wider and straighter than they will be in adults, with robust musculature to protect from abrasion from vascular plants (*Gullan PJ & Cranston PS, 2014*).

Ebenman's comprehensive mathematical studies reveal that strong intraspecific competition has a destabilising effect in populations where density is mainly dependent on adult reproduction as opposed to juvenile survival. Therefore, species with large ecological segregation between life stages (such as holometabolous insects) will be more stable (*Ebenman B, 1987*). In further studies, Ebenman reveals that when the difference between resources is larger between juvenile and adult stages, selection favours morphologies which result in high efficiency of resource utilisation by juveniles (*Ebenman B, 1992*). This may explain why the larvae are so specialised for consumption, as the food resources switch dramatically from solid-plant in larvae to liquid-plant in adults (*Gullan PJ & Cranston PS, 2014*).

These dramatically different morphologies and phenotypic traits among separate life stages characterize holometabolous development and are one of the main advantages over other developmental processes in insects. It benefits the species by allowing different stages to independently evolve to separate distinct niches, thus reducing intraspecific competition and increasing population survival and thus reproductive success.

### Potential for Protracted Diapause

Holometabolous insects experience a pupal stage where they are largely inactive. This stage is concerned with connecting the gap between the feeding stages and an adult specialized for distribution and reproduction (*Hinton HE, 1963*). Despite this being the primary purpose, the stage can also be used as a potential to extend diapause. Diapause is a period of dormancy in response to times of adverse environmental conditions. Diapause may also be necessary to extend a short life cycle to a full year

in univoltine insects (*Gullan PJ & Cranston PS, 2014*).

The presence of a pupal stage in holometabolous development is advantageous as it is a suitable period in which diapause may be prolonged. This is because during this time, the stage is in a relatively closed system with only the exchange of gases taking place, thus allowing better survival during times of environmental stress (*Gullan PJ & Cranston PS, 2014*).

### Energetically Expensive and Risk of Predation

Although there are many advantages to holometaboly, the disadvantageous consequences of the life cycle must also be revised. One disadvantage is that pupation is a highly energetically expensive process. The entire body must be remodeled as well as highly specific processes which carry high risk if completed incorrectly. For example, this includes the maintenance of beneficial symbiotic bacteria when the gut lining is remodeled instead of pathogenic microorganisms (*McMahon DP & Hayward A, 2016*).

As well as this, the sessile stage of pupation renders individuals immobile and defenseless to predation and parasitism. Pupae are mainly preyed upon by predatory insects and small mammals (*Frank JH, 1967*). Pupae may also be subject to parasitism, such as the endoparasitoid wasp *Pteromalus puparum*, which lays 150 eggs per gram on the pupae of Lepidoptera species that will hatch and feed on the pupa's tissues (*Godfray HCJ, 1994*).

### Conclusion

Despite some disadvantages of holometabolous development, the complex life cycles are clearly adaptively beneficial and successful. The holometabola comprise 60% of all defined animal species, containing more species than there are among animals or all other plant phyla combined (*McMahon DP & Hayward A, 2016; Engel MS, 2015*). The distinction between separate life stages, thus eliminating intraspecific competition, as well as the structural specialization within these stages are the key reasons enabling success in holometabolous development.

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