

---

Article

# The importance of trans-generational effects in Lepidoptera

Luisa WOESTMANN\* and Marjo SAASTAMOINEN

Metapopulation Research Centre, Department of Biosciences, University of Helsinki, Finland

\*Address correspondence to Luisa Woestmann. E-mail: luisa.woestmann@helsinki.fi.

Received on 13 November 2015; accepted on 16 February 2016

## Abstract

The importance of trans-generational effects in shaping an individuals' phenotype and fitness, and consequently even impacting population dynamics is increasingly apparent. Most of the research on trans-generational effects still focuses on plants, mammals, and birds. In the past few years, however, increasing number of studies, especially on maternal effects, have highlighted their importance also in many insect systems. Lepidoptera, specifically butterflies, have been used as model systems for studying the role of phenotypic plasticity within generations. As ectotherms, they are highly sensitive to environmental variation, and indeed many butterflies show adaptive phenotypic plasticity in response to environmental conditions. Here, we synthesize what is known about trans-generational effects in Lepidoptera, compile evidence for different environmental cues that are important drivers of trans-generational effects, and point out which offspring traits are mainly impacted. Finally, we emphasize directions for future research that are needed for better understanding of the adaptive nature of trans-generational effects in Lepidoptera in particular, but potentially also in other organisms.

**Key words:** butterfly, maternal effect, moth, offspring quality, paternal effect, plasticity.

---

## Introduction

An individuals' phenotype is influenced by its genotype, the environmental conditions it experienced during its development but often also by the environmental conditions experienced by its parents (Mousseau and Fox 1998; Talloen et al. 2004; Refsnider and Janzen 2010). Phenotypic plasticity, defined by 1 genotype generating different phenotypes depending on the environmental conditions, is thought to represent an adaptive response to predictable environmental variation when the modification improves individuals' performance.

Similarly, trans-generational effects are considered adaptive when parents can match the offsprings' phenotype to changes in the environment, thereby buffering their offspring from environmental stressors (Mousseau and Dingle 1991; Agrawal et al. 1999). Such predictive adaptive responses where the response to a cue has an advantage later in life are important in a number of organisms including humans. Human fetus developing under maternal under-nutrition or stress during gestation may result in small offspring with permanently altered metabolism (Gluckman et al. 2005). Rather than being an inevitable consequence of a poor environment,

such alteration in the offspring phenotype may actually confer an advantage under similar future environment (Gluckman et al. 2005). Moreover, quality of the diet not only affects offspring but sometimes even the second generation, potentially in a gender-dependent manner (Pembrey et al. 2006). Hence, seemingly simple cues can have a big influence on the offspring or even later generations. Trans-generational effects might not always be adaptive, however, the "prediction" by the parent may not be the best possible one, resulting in a parent-offspring conflict (i.e., responses may be disadvantageous for the parent, the offspring or both; Uller 2008). In the human example described above, a negative consequence of the altered phenotype has been suggested (e.g., development of metabolic syndrome and type II diabetes) when there is a mismatch between the predicted and realized future environment (see Rickard and Lummaa 2007 for further discussion). Adaptive trans-generational effects are predicted to evolve only when there is enough temporal or spatial environmental heterogeneity in both generations, and when the conditions experienced by the offspring are predictable from the parent generation (via environment or phenotype; Uller 2008; Leimar and

McNamara 2015). In addition, the costs for receiving information from the environment, transmitting them to the offspring, and responding to the cues need to be low enough for both generations (Uller 2008; van den Heuvel et al. 2013).

### Butterflies as Good Models for Studying the Importance of Trans-generational Effects

Most research on maternal effects has been conducted on plants and vertebrates (Agrawal et al. 1999). During the past two decades, an increasing number of trans-generational studies have also been conducted on invertebrates, particularly insects (Mousseau and Dingle 1991; Roth et al. 2010). There are multiple advantages to study trans-generational effects in insects, including their relatively short-generation times and ease to rear in the laboratory. Moreover, as ectotherms, insects are very sensitive to their surrounding environment, and are thus influenced by the external factors that trans-generational effects help to mitigate. Lepidoptera in particular have been used as model systems for within-generation phenotypic plasticity studies (see Box 1), and evidently adaptive plastic responses to various environmental conditions are of crucial importance in a number of species. Based on this importance of phenotypic plasticity and seasonal polyphenism in Lepidoptera, one could, therefore, assume that adaptive trans-generational effects are of equal importance in these species (but see also Leimar and McNamara 2015 for how different circumstances may favor the different type of cue or phenotype determination). Assessing predictive adaptive trans-generational responses in species experiencing seasonal, and therefore predictable, environments is reasonable, and logistically doable when cues predicting the environmental change can easily be assessed in nature as well as manipulated in the laboratory. Moreover, the ecology, including generation time, resource specificity and phenology, of Lepidoptera is often well-understood, allowing researchers to make more specific predictions about the potential importance of trans-generational effects in their species of interest.

Here, we will review what is known about the importance of trans-generational effects in Lepidoptera, which factors have been studied most, and identify some results that may be generalized. Based on theory, one could also test whether adaptive trans-generational effects are more or less common in species with seasonal polyphenism, in multivoltine species, or when the conditions of parents predict conditions of offspring in a more honest manner.

We will finish with highlighting the interesting future avenues for research on trans-generational effects to those working with Lepidoptera but also emphasize how such studies could help us to validate theoretical predictions of the evolution of trans-generational effects in more general. We focus our assessment in studies that have measured offspring quality in response to some parental effect and hence in most parts exclude studies that only assess number of eggs and larvae. Finally, this review is not exhaustive, as we mainly reviewed studies that included maternal, paternal, or trans-generational terms in their abstract. Here, we will synthesize information from around 45 papers (Table 1).

### Thermal Environment as the Main Abiotic Cue for Trans-Generational Effects

As ectotherms, Lepidoptera are highly susceptible to changing climatic conditions. It is, therefore, not surprising that many studies

have investigated trans-generational effects in response to thermal conditions.

It seems evident, that in many cases mothers adjust resource allocation to their offspring in relation to cool thermal conditions. In seasonally polyphenic *Bicyclus anynana* and in the geographically polyphenic *Pararge aegeria*, mothers experiencing cooler thermal conditions lay larger but fewer eggs (Fischer et al. 2003a, 2003b; Geister et al. 2009; Gibbs et al. 2010b), which in turn results in higher hatching success and larger larvae (Fischer et al. 2003a, 2003b; Geister et al. 2009). The offspring of mothers exposed to a colder environment may also have shorter development time and a higher probability to reach maturity (Fischer et al. 2003a). These results are in accordance with the general temperature-size rule, stating that organisms should grow larger in colder environments when growth efficiency is decreasing with increasing environmental temperature (Atkinson et al. 2006). Moreover, thermal conditions can also change the resource provisioning to the eggs, which can translate to the larval composition (Geister et al. 2009).

The impact of higher temperatures or even drastic heat shock for a shorter period during the parental adulthood on the offspring are, as expected, the opposite: egg numbers increase while egg size decreases (Steigenga and Fischer 2007; Janowitz and Fischer 2011). The responses on hatching success are somewhat contradictory, as the hatching success either decreases (Zhang et al. 2013) or it is not affected by increased thermal conditions experienced by the mothers (Janowitz and Fischer 2011). This discrepancy may be due to the temperature treatments (drastically higher but shorter in Janowitz and Fischer 2011) or the ecology of the species. Paternal effects were assessed in very few studies, with one finding no effect on egg size (Fischer et al. 2003b) and the other two finding small effects on egg fertility, egg mass, and size (Janowitz and Fischer 2011; Zhang et al. 2013).

The majority of the studies focused solely on maternal effects (but see Fischer et al. 2003b; Janowitz and Fischer 2011; Zhang et al. 2013), and investigated the effect of temperature during the reproductive adult stage only. Few studies did, however, investigate the possible predictive adaptive response by assessing responses also under different thermal conditions on the offspring (Fischer et al. 2003a, 2003b; Steigenga and Fischer 2007; Geister et al. 2009; Gibbs et al. 2010b). The tropical butterfly, *B. anynana*, exhibits seasonal polyphenism with the two morphs showing striking differences in a number of morphological and life-history traits, as an adaptation to alternative wet–dry seasonal environments (Pijpe et al. 2007). The egg size in *B. anynana* is also plastic, with larger eggs being produced under cooler thermal conditions (dry season). This response seems adaptive, as under cooler conditions the larger eggs also have higher hatching success, larger hatchlings, and a higher probability to reach maturity (Fischer et al. 2003a). *Bicyclus anynana* could be a particularly suitable organism to study the adaptive nature of trans-generational effects, as it encounters a regular and predictable seasonal change, yet in which the honesty of the cue may depend on the developmental stage of the individual.

Photoperiod is an abiotic factor that has been neglected in trans-generational studies of Lepidoptera, even though it has been studied in within-generation plasticity in butterflies in regards to morph development and diapause (Nylin 1992; Sakamoto et al. 2015), and in regards to trans-generational effects in other insects (Saunders 1966; Giesel 1986). It would be interesting to see if photoperiodic variation would have consequences for the offspring, as has been found in other insects and might be expected based on its relevance for within-generation plasticity and seasonal polyphenism.

**Box 1. Seasonal polyphenism and adaptive phenotypic plasticity in butterflies**

Seasonal polyphenism is a form of plasticity where discrete phenotypes arise from a single genotype in response to differing environmental conditions (Moran 1992). Seasonal polyphenism is quite common in butterflies and often induced by thermal conditions, but in some cases changes in photoperiod are also required as a cue to induce the development of the different morphs. In addition, the level of polyphenism varies across species. Some phenotypic responses are rather subtle, for example changes in melanization and darkness of the wing in response to thermal conditions (e.g. *Pieris* butterflies and *Pararge aegeria*; Kingsolver and Wiernasz 1991).

In many cases, however, the alternating phenotypes differ quite substantially from each other (Fig. 1). In Lepidoptera, the seasonal polyphenism and its regulation is probably best characterized in the tropical butterfly, *Bicyclus anynana* (Brakefield et al. 1998, Beldade and Brakefield 2002). *B. anynana* is known to exhibit phenotypic plasticity as an adaptive response to wet-dry seasonal environments. The two seasonal morphs differ in morphology and wing pattern (especially in the size of eyespots on the ventral wings) but also in number of life-history traits (Pijpe et al. 2007). The cue of the developmental switch is the thermal conditions during larval development. When larvae are reared under warm thermal conditions they develop into the wet-season morph, which is characterized by large eyespots, shorter development time, smaller body size, faster reproduction, and a shorter lifespan compared with the dry-season morph (e.g., Brakefield and Reitsma 1991, Thompson and Pellmyr 1991, Pijpe et al. 2006). The polyphenic differences between the two adult morphs are programmed by hormonal regulation of ecdysteroids and juvenile hormones during development (Oostra et al. 2011).

In the temperate region butterfly seasonal polyphenism is well-characterized, for example, for the comma butterfly (*Polygonia c-album*; Karlsson et al. 2008), the speckled wood butterfly (*Pararge aegeria*; Agrawal 2002, van Dyck and Wiklund 2002) and the map butterfly (*Araschnia levana*; Friberg and Karlsson 2010, Fig 1). In both of these species the polyphenism is also related to multivoltinism and seasonality, and namely the potential induction of the over-wintering (diapausing) morph. Hence, these species have a reproductively active and shorter lived summer morph (sometimes several) which is induced by longer photoperiod and higher temperatures. The diapausing morphs, on the other hand, are induced by shorter day length and lower temperatures (in *P. aegeria* the photoperiod is more important as the cue). An additionally interesting aspect of these species is the variation in phenotypic plasticity among southern and northern populations (Gotthard et al. 1994).



**Figure 1.** Seasonal morphs of the tropical butterfly *Bicyclus anynana* (wet-season morph (top left) and dry-season morph (bottom left)) and the temperate butterfly *Araschnia levana* (spring morph (top right) and summer morph (bottom right)). Pictures by Oskar Brattstrom (wet-season morph), Andre Coetzer (dry-season morph), Juha Sormunen (spring morph) and Tari Haahtela (summer morph).

**Key Biotic Factors that Influence Trans-Generational Effects**

It seems that even though temperature plays an important role in the life history of most Lepidoptera, the influence of biotic factors on trans-generational effects have been studied much more extensively. Below, we review the results based on the type of biotic factor that was used as a cue but it was notable that many studies in fact combined multiple cues. Moreover, oviposition-site choice represents a maternal effect that has a great impact on the offspring performance. However, we have excluded studies investigating effects of oviposition-site choice from this review as several reviews already exist on this unique and important cue (Box 2 provides an overview on the main hypotheses).

**Nutrition**

When it comes to trans-generational effects, the influence of nutrition is probably the most studied environmental condition in all organisms. Nutrition in Lepidopteran systems is used as a proxy for resource availability, both during development and during the adult stage. Direct impacts of nutrition on resource allocation and adult life history variation have also been extensively studied in *Speyeria mormonia* (Boggs and Ross 1993; Boggs and Freeman 2005; Niitepöld et al. 2014), *Melitaea cinxia* (Saastamoinen et al. 2013a), *P. aegeria* (Gibbs et al. 2012), and *B. anynana* (Bauerfeind and Fischer 2005; Saastamoinen et al. 2010; Saastamoinen et al. 2013b). The resource allocation and egg composition is impacted by both larval and adult diet (Boggs 1997; Boggs and Niitepöld 2014), indicating that maternal effects in response to food

**Table 1.** An overview of the traits affected in different species of Lepidoptera, mentioning direction and which parental cue is causing the effect

|                        | Trait affected      | Direction  | Species   | References   |   |
|------------------------|---------------------|--|---|--|---|
| <i>Abiotic</i>         | High temperature    | Egg fertility  | ↓   | <i>Helicoverpa armigera</i>  | Mironidis and Savopoulou-Soultani (2010)                                    |
|                        |                     | Egg mass   | ↓   | <i>Bicyclus anynana</i>  | Janowitz and Fischer (2011)   |
|                        |                     | Egg size   | ↓   | <i>Bicyclus anynana</i>  | Janowitz and Fischer (2011)   |
|                        |                     | Hatching success   | ↓   | <i>Plutella xylostella</i>   | Zhang et al. (2013)   |
|                        | Low temperature     | Egg composition  | ↑   | <i>Pararge aegeria</i>   | Gibbs et al. (2010b)  |
|                        |                     |  | –   | <i>Bicyclus anynana</i>  | Janowitz and Fischer (2011)   |
|                        |                     | Egg size   | –   | <i>Bicyclus anynana</i>  | Geister et al. (2009)   |
|                        |                     |  | a   | <i>Pararge aegeria</i>   | Gibbs et al. (2010b)  |
|                        |                     | Egg mass   | ↑   | <i>Bicyclus anynana</i>  | Fischer et al. (2003b); Steigenga and Fischer (2007); Geister et al. (2009) |
|                        |                     |  | ↓   | <i>Pararge aegeria</i>   | Gibbs et al. (2010b)  |
|                        |                     |  | ↑   | <i>Pararge aegeria</i>   | Gibbs et al. (2010b)  |
|                        |                     |  | ↑   | <i>Pararge aegeria</i>   | Gibbs et al. (2010b)  |
|                        |                     |  | ↑   | <i>Bicyclus anynana</i>  | Fischer et al. (2003a)  |
|                        |                     |  | ↑   | <i>Bicyclus anynana</i>  | Fischer et al. (2003a); Geister et al. (2009)                               |
|                        |                     |  | ↑   | <i>Bicyclus anynana</i>  | Geister et al. (2009)   |
| <i>Biotic</i>          | Good food quality   | C/N ratio  | –   | <i>Lasiommata megera</i>   | Mevi-Schütz and Erhardt (2003)  |
|                        |                     | Egg composition  | a   | <i>Bicyclus anynana</i>  | Karl et al. (2007); Geister et al. (2008)                                   |
|                        |                     |  | a   | <i>Lymantria dispar</i>  | Rossiter et al. (1993)  |
|                        |                     | Egg developmental time                                       | –   | <i>Coenonympha pamphilus</i>   | Cahenzli and Erhardt (2013a)  |
|                        |                     | Egg size   | ↑   | <i>Bicyclus anynana</i>  | Bauerfeind et al. (2007)  |
|                        |                     | Egg mass   | –   | <i>Choristoneura fumiferana</i>  | Carisey and Bause (2002)  |
|                        |                     | Hatching success   | ?   | <i>Lymantria dispar</i>  | Rossiter et al. (1993)  |
|                        |                     |  | ↑   | <i>Hyphantria cunea</i> ,<br><i>Bicyclus anynana</i> ,<br><i>Coenonympha pamphilus</i> | Morris (1967); Geister et al. (2008); Cahenzli and Erhardt (2012)           |
|                        |                     | Larval hatching mass   | –   | <i>Lasiommata megera</i> ,<br><i>Coenonympha pamphilus</i>                             | Mevi-Schütz and Erhardt (2003); Cahenzli and Erhardt (2013a)                |
|                        |                     |  | ↑   | <i>Coenonympha pamphilus</i>   | Cahenzli and Erhardt (2013a)  |
|                        | ↑                   |  | <i>Heliothis virescens</i>                            | Gould (1988)   |   |
|                        | ↑/↓                 |  | <i>Lymantria dispar</i>                               | Rossiter (1991)  |   |
|                        | ↑                   |  | <i>Coenonympha pamphilus</i>                          | Cahenzli and Erhardt (2012)  |   |
|                        | Poor food quality   | Immunity   | –   | <i>Malacosoma pluviale californicum</i>  | Myers et al. (2011)   |
|                        |                     |  | ↓   | <i>Melitaea cinxia</i>   | Saastamoinen et al. (2013a)   |
| Female/male sex-ratio  |                     | ↑  | <i>Danaus plexippus</i>                               | Sternberg et al. (2015)  |   |
|                        |                     | ↓  | <i>Lymantria dispar</i>                               | Erelli and Elkinton (2000)   |   |
| Offspring survival     |                     | ↑  | <i>Hyphantria cunea</i>                               | Morris (1967)  |   |
|                        |                     | –  | <i>Lasiommata megera</i> ,<br><i>Bicyclus anynana</i> | Mevi-Schütz and Erhardt (2003); Geister et al. (2008)                                  |   |
| Egg developmental time |                     | ↓  | <i>Operophtera brumata</i>                            | van Asch et al. (2010)   |   |
|                        |                     | ↓  | <i>Pieris rapae</i>                                   | Rotem et al. (2003)  |   |
|                        |                     | ↓  | <i>Lymantria dispar</i> ,<br><i>Bicyclus anynana</i>  | Erelli and Elkinton (2000); Bauerfeind and Fischer (2005); Saastamoinen et al. (2010)  |   |
|                        |                     | a  | <i>Danaus plexippus</i>                               | Sternberg et al. (2015)  |   |
|                        | ↓                   | <i>Choristoneura fumiferana</i> ,<br><i>Bicyclus anynana</i> | Carisey and Bause (2002); Bauerfeind et al. (2007)    |  |   |
|                        | ↑                   | <i>Melitaea cinxia</i>                                       | Saastamoinen et al. (2013a)                           |  |   |
|                        | ↓                   | <i>Pieris rapae</i>  | Rotem et al. (2003)                                   |  |   |
|                        | –                   | <i>Lymantria dispar</i>                                      | Erelli and Elkinton (2000)                            |  |   |
|                        | ↓                   | <i>Plodia interpunctella</i>                                 | Triggs and Knell (2012)                               |  |   |
|                        | ↓                   | <i>Lymantria dispar</i>                                      | Keena et al. (1998)                                   |  |   |
|                        | ↓                   | <i>Choristoneura fumiferana</i>                              | Carisey and Bause (2002)                              |  |   |
|                        | ↑                   | <i>Melitaea cinxia</i>                                       | Saastamoinen et al. (2013a)                           |  |   |
| ↓                      | <i>Pieris rapae</i> | Rotem et al. (2003)  |   |  |   |

(continued)

**Table 1.** Continued

|   | Trait affected                     | Direction                         | Species   | References   |
|---|------------------------------------|-----------------------------------|---|--|
| <b>If offspring experiences same conditions as parent</b> | Pupal mass                         | ↑                                 | <i>Lymantria dispar</i>   | Rossiter (1991)  |
|   | Offspring performance              | ↑                                 | <i>Pieris rapae</i>   | Cahenzli et al. (2015)   |
|   | Developmental time                 | ↑                                 | <i>Coenonympha pamphilus</i>                                    | Cahenzli and Erhardt (2013b)   |
|   | Pupal mass                         | ↑                                 | <i>Coenonympha pamphilus</i>                                    | Cahenzli and Erhardt (2013b)   |
| <b>Increasing age</b>                                     | Offspring survival                 | ↑                                 | <i>Choristoneura fumiferana</i> ,<br><i>Plutella xylostella</i> | Carisey and Bauce (2002);<br>Henniges-Janssen et al. (2011)                            |
|   | Tolerance to starvation            | ↑                                 | <i>Choristoneura fumiferana</i>                                 | Carisey and Bauce (2002)   |
|   | Forewing size                      | ↑                                 | <i>Coenonympha pamphilus</i>                                    | Cahenzli and Erhardt (2013b)   |
|   | Egg fertility                      | ↓                                 | <i>Pararge aegeria</i>  | Wiklund and Persson (1983)   |
|   | Egg size                           | ↓                                 | <i>Pararge aegeria</i> ,<br><i>Lasiommata megera</i>            | Wiklund and Persson (1983);<br>Mevi-Schütz and Erhardt (2003);<br>Gibbs et al. (2010c) |
|   | Egg survival until adult emergence | ↓                                 | <i>Pieris brassicae</i>   | Ducatez et al. (2012)  |
| <b>Low density Density/infection</b>                      | Egg mass                           | ↓                                 | <i>Lasiommata megera</i> ,<br><i>Pararge aegeria</i>            | Mevi-Schütz and Erhardt (2003);<br>Gibbs et al. (2010b)                                |
|   | Embryonic developmental time       | ↑                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010c)   |
|   | Hatching success                   | ↓                                 | <i>Bicyclus anynana</i>   | Bauerfeind et al. (2007)   |
|   | Larval mass                        | ↓                                 | <i>Bicyclus anynana</i>   | Kehl et al. (2015)   |
|   | Offspring adult life span          | ↓                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010c)   |
|   | Sperm number                       | ↑                                 | <i>Pieris brassicae</i>   | Ducatez et al. (2012)  |
|   | Spermatophore mass                 | ↑                                 | <i>Bicyclus anynana</i>   | Kehl et al. (2015)   |
|   | Female/male sex-ratio              | ↑                                 | <i>Bicyclus anynana</i>   | Kehl et al. (2015)   |
|   | Egg viability                      | –                                 | <i>Lymantria dispar</i>   | Myers et al. (1998)  |
|   |                                    |                                   | <i>Malacosoma pluviale californicum</i>                         | Rothman (1997)   |
| <b>Increased flight activity</b>                          | Larval developmental time          | –                                 | <i>Malacosoma pluviale californicum</i>                         | Rothman (1997)   |
|   | Mortality                          | –                                 | <i>Malacosoma pluviale californicum</i>                         | Rothman (1997)   |
|   | Pupal mass                         | ↑                                 | <i>Malacosoma pluviale californicum</i>                         | Rothman (1997)   |
|   | Egg size                           | ↓                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010a)   |
|   | Egg to pupa survival               | –                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010a)   |
| <b>Flight/temperature</b>                                 | Hatching success                   | ↓                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010a)   |
|   | Larval developmental time          | ↑                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010a, 2010c)  |
|   | Larval mass                        | ↓                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010c)   |
|   | Immunity                           | ↓                                 | <i>Pararge aegeria</i>  | Gibbs et al. (2010c)   |
| <b>Infection of parent generation</b>                     | Flight metabolic rate              | <sup>b</sup>                      | <i>Melitaea cinxia</i>  | Mattila and Hanski (2014)  |
|   | Resting metabolic rate             | <sup>b</sup>                      | <i>Melitaea cinxia</i>  | Mattila and Hanski (2014)  |
| <b>Larger or more nuptial gifts</b>                       | Developmental time                 | ↑                                 | <i>Trichoplusia ni</i>  | Freitak et al. (2009)  |
|   | Immunity                           | ↑                                 | <i>Trichoplusia ni</i>  | Freitak et al. (2009)  |
|   | Susceptibility to viral exposure   | ↓                                 | <i>Plodia interpunctella</i>                                    | Tidbury et al. (2011)  |
| <b>Oviposition</b>  | Mortality                          | ↑                                 | <i>Trichoplusia ni</i>  | Freitak et al. (2009)  |
|   | Egg mass                           | ↑                                 | <i>Pieris napi</i>  | Wiklund et al. (1993)  |
| <b>Oviposition</b>  | Reproductive effort                | –                                 | <i>Pararge aegeria</i>  | Wedell and Karlsson (2003)   |
|   | Growth                             | ↑                                 | <i>Pieris napi</i>  | Wedell and Karlsson (2003)   |
|   | Oviposition-choice                 | <sup>a</sup>                      | <i>Danaus plexippus</i>   | Ladner and Altizer (2005)  |
|   | Offspring survival                 | Adapt offspring to own host plant | <i>Pieris rapae</i>   | Cahenzli et al. (2015)   |
|   |                                    | <sup>a</sup>                      | <i>Danaus plexippus</i>   | Ladner and Altizer (2005)  |

<sup>a</sup> Change detected, direction not specified (for details see Supplementary Table 1).

<sup>b</sup> Animal model study: flight metabolic rate is heritable whereas resting metabolic rate underlies a strong maternal effect.

limitation may be very important. Food quality manipulations are extremely variable among the studies, ranging from elegant changes in the supplemented amino acids, and variation in the amounts of proteins, lipids, or other chemical compounds, to studies that examine the effects of complete or partial starvation—thus, making any generalization of the results difficult.

Poor dietary conditions experienced by the parents during either their development or during their reproductive stage generally lead to decreased fecundity (Morris 1967; Bauerfeind and Fischer 2005; Myers et al. 2011) but in some cases also to larger offspring (Morris 1967; Rotem et al. 2003; Geister et al. 2008). Some studies show changes in egg composition (Karl et al. 2007), reduced egg viability

### Box 2. A challenging decision? Oviposition-site-choice as a unique maternal effect

Oviposition-site-choice defines the selection of a site by an oviparous animal to deposit its eggs. There are several reviews available that have dealt with oviposition behavior and host preference in Lepidoptera, as well as summarized the hypotheses for variation in oviposition-site-choice in oviparous species in general (see Chew and Robbins 1984, Thompson and Pellmyr 1991). Here, we will present a short overview on oviposition-site-choice as a potential source of trans-generational effects in Lepidoptera.

Oviposition-site-choice represents an important maternal effect by which mothers can influence the phenotype and survival of their offspring (Bernardo 1996). Apart from potentially having tremendous effect on offspring survival, the mother's decision on where to lay her eggs can also affect juvenile performance and phenotype (Resetarits 1996). Choosing sites that minimize predation risk or offer a suitable microclimate for the embryonic development may help to ensure offspring survival. Moreover, avoiding oviposition on plants that already possess eggs of the same species helps to ensure offspring survival, as competition between larvae of conspecifics or related species will be avoided (e.g. Schoonhoven et al. 1990, Brakefield and French 1993). Oviposition on ideal host plants or ideal microhabitat increases also juvenile performance, as the offspring are likely to develop faster under better quality host plants and under optimal microclimatic conditions (Nylin and Gotthard 1998, Priest et al. 2008). Moreover, optimal host plants might provide offspring possibilities to hide from predators and also obtain beneficial chemical compounds as e.g. defensive chemicals, which they can use against their own predators (reviewed in Refsnider and Janzen 2010).

The preference to oviposit on host plants with the highest nutritional quality is outlined in the preference-performance hypothesis. However, it has been shown that oviposition-site-choice in many Lepidoptera does not always occur according to this hypothesis, i.e. the mothers don't always choose the "best possible" host plant from the perspective of their offspring. This is the case for example in the pierid butterfly (*Anthocharis cardamines*) in which females often oviposit on host plants with poor nutrition from the offspring perspective. This results in higher maternal fitness/survival due to lower search effort but not optimization of the quality of the offspring (Courtney 1981). A similar result was found in the fall webworm (*Hyphantria cunea*) where host abundance represents a predictor of host use, suggesting a selective pressure for a reduction in searching time for oviposition sites (Murphy and Loewy 2015). In the Åland islands, the Glanville fritillary butterfly (*M. cinxia*) uses two hosts: *Plantago lanceolata* and *Veronica spicata* (Fig. 2). This butterfly evolves local adaptation in form of oviposition preference for one of those hosts (Kuussaari et al. 2000). Another study revealed that based on survival data, butterflies should use the two host plants in relation to their abundance whereas lab experiments suggested they should have a clear preference for one of them (*Veronica spicata*). Neither was the case, suggesting that larval survival and growth are not the driving forces for the decision (Van Nouhuys et al. 2003). Such decisions might result from a conflict between parent and offspring. Females might be time-limited in the search of a suitable host plant due to a trade-off between search time and feeding time (Mayhew 2001).



**Figure 2.** The Glanville fritillary butterfly (*Melitaea cinxia*, female) and its two host plants *Veronica spicata* (right) and *Plantago lanceolata* (left). Pictures by Luisa Woestmann (host plants) and Ilkka Hanski (butterfly).

(Carisey and Bauce 2002), but also faster egg development (van Asch et al. 2010), if parents experienced poor nutritional conditions during their development. Responses are often species-specific but some indicate positive and adaptive responses under food-limited conditions. Survival of the larvae in response to maternal nutritional conditions is less studied but in 1 case a negative response was found (Carisey and Bauce 2002). Parental diet influences also offspring immunity, without any particular direction, however: poor quality diet has been shown to reduce immunity (*Plodia interpunctella*; Triggs and Knell 2012) or to have no effect (*Malacosoma pluviale californicum*; Myers et al. 2011). The negative effects of poor diet are more prominent if both parents (Triggs and Knell 2012) and generations (Keena et al. 1998) experience them. In the gypsy moth *Lymantria*

*dispar*, dietary conditions influence the offspring sex-ratio, as mothers with poor diet during development had a higher percentage of males in their progeny (Erelli and Elkinton 2000), potentially indicating that the costs of producing male and female offspring differ.

Improvement in food quality during the reproductive stage increases offspring quality in terms of increased hatching success (Cahenzli and Erhardt 2012), whereas improved food quality during development of the mother increases offspring number but reduces offspring size (Rotem et al. 2003). The offspring of high food quality mothers may also show faster development (Rotem et al. 2003). Again the direction of the change in offspring body size is not always the same. Interestingly, parent sex-specific trans-generational effects have also been found, resulting, for example, in effects only being

present if mother or father experienced a certain diet (Gould 1988; Cahenzli and Erhardt 2012).

Even though still infrequent, the paternal effects have also been studied more in the context of nutrition than in the context of other environmental cues. Improved food quality of fathers increases offspring mass and offspring resistance to a parasitic infection (Cahenzli and Erhardt 2013a; Sternberg et al. 2015). Very few studies again have investigated the possible adaptive responses in the offspring. However, a few studies suggest that parents seem to adapt their offspring to the conditions they experienced themselves. This has been shown in case of low quality food (*Choristoneura fumiferana*; Carisey and Bauce 2002), starvation during development (*M. cinxia*; Saastamoinen et al. 2013a), plant defense components (*H. virescens*; Gould 1988), or amounts of protein in the diet (*Pieris rapae*; Rotem et al. 2003), as well as a general adaptation to the same host plant type (*P. rapae*; Cahenzli et al. 2015). These studies reflect classic examples for predictive adaptive responses that are able to buffer offspring from environmental changes or stressors. However, the future environment might not always be the same for parent and offspring, possibly resulting in maladaptive responses. Such mismatch between the predicted environment and that experienced by the offspring may be more likely in species with a univoltine life cycle. Bet-hedging could also occur as a strategy to produce a wide variety of different offspring phenotypes to spread the risk that 1 type of phenotype does not survive (Krug and Zimmer 2000; Krug 2001).

The predominant usage of different dietary treatments during developmental stage rather than reproductive stage in general may stem from the studies of within-generation plasticity (see Box 1). In general, the adaptive trans-generational effects in regards to nutrition seem to be important in species with different ecology, as they have been observed in uni- and multivoltine species, as well as in seasonally polyphenic species. However, the magnitude of the importance could still be different among species or within species when comparing different generations or populations that vary in seasonality, for example. As far as we know, such comparisons have not been conducted so far.

### Nuptial gifts

In many insects, including Lepidoptera, males transfer spermatophores during mating that contain not only the sperm, but also accessory gland secretions, which contain nutrients that get incorporated by the female into eggs and soma (Boggs and Gilbert 1979). Increased spermatophore size often increases female fecundity and life span (Gwynne 1988; Simmons 1990; Oberhauser 1997) and hence, male nuptial gifts represent a paternal investment, whereby it increases the number of surviving progeny by increasing the reproductive output of a female either via number of offspring or via the quality of the offspring (Wiklund et al. 1993). Factors such as poor nutritional and mating status, and the age or size of the male can influence spermatophore size and composition (Svärd and Wiklund 1989; Wiklund and Forsberg 1991). Already mated males produce a smaller second spermatophore, especially when the frequency between the matings is short (Kaitala and Wiklund 1995). Most studies on nuptial gifts focus only on the direct impacts of spermatophore size on the number of eggs produced and surprisingly few studies have looked at the quality of the offspring. The study by Cahenzli and Erhardt (2013a) showed that male nutrition influences offspring hatching mass. Amino acid supplements in nectar increased spermatophore quality that in turn influenced offspring quality. However, spermatophore size or sperm quality was not assessed directly. In any case nuptial gifts are evidently important

components of paternal investments on offspring quality and more studies should be conducted on this front.

### Flight

Flight is extremely costly due to the high energetic demand and physiological stress. As life history theory predicts trade offs between costly traits, a number of studies have assessed fitness, namely reproductive (flight-oogenesis-syndrome; Baguette and Schtickzelle 2006), costs related to flight in butterflies (Bonte et al. 2012). Forced flight can lead to smaller eggs, resulting in reduced hatching success, lower larval mass, and a longer developmental time in the speckled wood butterfly (Gibbs et al. 2010a). Additionally, offspring from the flight treated mothers showed reduced survival upon Baculovirus infection, indicating that they were of lower quality (Gibbs et al. 2010c). Similarly, increased flight in *Pieris brassicae* decreases egg and offspring number, as well as egg survival with some interaction with paternal age (Ducatez et al. 2012).

### Density

Several within-generation studies have assessed the effects of density and found influence on, for example, sex-ratio (Campbell 1963a, 1963b; Myers et al. 1998). Yet, very few have assessed potential trans-generational effects. Combining different density histories from wild-collected parent individuals and infection with Baculovirus in the lab resulted in no effect on hatching success, survival of the offspring, or on pupal mass of male progeny in the western tent caterpillar *M. californicum*. However, in female progeny highest pupal mass was obtained at low density with no presence of the virus (Rothman 1997). The result may be explained by reduced competition for food during the larval stage or lack of trade off between infection and development and may translate to higher survival rates in females.

Density might represent an important factor in terms of trans-generational effects, as it has been shown to influence, for example, sex-ratio (see above). Potentially, the impact of density on trans-generational effects may depend on whether the species is solitary or gregarious during development. For example, in species where larvae live gregariously, higher density might induce higher immune response (Kong et al. 2013, but see Piesk et al. 2013). Similarly, individuals from populations with different density background could show different adaptive responses.

### Immunity

Trans-generational immune priming represents the transmission of increased immunity from immune-challenged parents to their offspring. Whereas this process occurs via transfer of maternal antibodies in vertebrates, it is less clear how the process works in invertebrates, as they do not possess antibodies. Insect immunity has long been assumed to lack memory or specificity (Klein 1989), but recent studies have revealed some opposite evidence (Roth et al. 2010). In beetles *Tribolium castaneum*, higher survival rate was found after a challenge with a lethal dose of live bacteria if they were once primed with heat-killed bacteria of the same strain in comparison to a group that was pricked with a different strain. Similar results have been obtained in other insects (Pham and Schneider 2008; Sadd and Schmid-Hempel 2008). Immune priming can also work across generations. Whereas in vertebrates antibodies can be transferred to the offspring only by mothers, in invertebrates immune priming can be achieved via mothers (Little et al. 2003;

Moret 2006; Freitak et al. 2009) but also via fathers (Roth et al. 2010; Zanchi et al. 2011).

Studies investigating the occurrence or importance of trans-generational immune priming in Lepidoptera are scarce. In the Indian mealmoth *P. interpunctella*, the offspring of parents that were exposed to a low viral dose were less susceptible to the same infection (Tidbury et al. 2011). The effect was not transferred to the F3 generation. In the cabbage semilooper *Trichoplusia ni*, the effects of constant ingestion of bacteria (*Escherichia coli* and *Micrococcus luteus*) during development of the parents on the immunity of their progeny was assessed (Freitak et al. 2009). The responses included several aspects of the immune response (e.g., protein expression, transcript levels, and enzyme activities). However, the trans-generational immune priming was only evident in few of the immune markers, highlighting the complexity of immune responses also in invertebrates.

Immunity is a very complex trait as it is highly sensitive to a number of factors in the environment, and large enough data sets can be hard to collect and difficult to interpret, for example, in regards to time series and tissue samples. Furthermore, natural pathogens of a species are often unknown, making it hard to decide on a pathogen or parasite to use. This often leads to very general bacterial treatments (Freitak et al. 2009). However, some viruses that are able to infect a wide range of Lepidopteran species are known, like Baculovirus. Adults of the monarch butterfly *Danaus plexippus* are commonly infected with the protozoan *Ophryocystis elektroscirrha* and show reduced fecundity under infection (de Roode et al. 2007), offering an interesting natural host–pathogen study system in which trans-generational factors may be important as well. As diseases can have a big impact on insect populations, studying the impact of trans-generational effects on immunity are very interesting and are of key importance.

## Conclusions

Our review highlights that trans-generational effects in Lepidoptera are important and ubiquitous in response to a number of different environmental cues. However, much of the research so far has been driven by and is the continuum of the findings regarding adaptive phenotypic plasticity, as well as resource allocation theory and life history trade offs in general. Uller (2008) emphasized in his review that in general there is a discrepancy between empirical and theoretical studies on trans-generational effects, as in that the former studies focus on whether or not parental effects occur or are adaptive, and in the latter the focus is on the consequences of parental effects for the short-term response of traits to selection.

Unfortunately, in the case of Lepidoptera studies we are still lagging behind, as most of the research still focuses simply on whether parental effects occur and under what circumstances and on what offspring traits they have an impact on. An increasing number of studies are, however, starting to look at whether the observed responses are adaptive and result in a fitness benefit for the offspring. We still found just 1 study that assessed the adult traits of the offspring generation (forewing length; Cahenzli and Erhardt 2013b). Similarly, to the best of our knowledge, none of the studies specifically consider under what conditions trans-generational effects would be selected on. In this front, however, butterflies could be extremely useful, and could bridge the gap between theory and empirical data. For example, testing some of the theoretical predictions by comparative studies on univoltine versus multivoltine species, or by comparing responses in different generations of the

multivoltine species could be extremely useful. In the latter case, for example, one would predict that early generations will be able to predict the future environment in a more honest way than the later generations of the year where the time interval between the generations is longer, leading to adaptive trans-generational effects being more likely in earlier generations. Finally, evolution of adaptive trans-generational effects are predicted, based on recent theoretic models, to be more likely with low levels of dispersal (Leimar and McNamara 2015). Here, Lepidoptera could again be useful model systems to test these predictions as dispersal is commonly studied, especially in butterflies, and known in some species to vary among local populations (Hanski et al. 2006; Hill et al. 2011). For example, comparing trans-generational effects between populations from core and expanding populations, which are known to differ in their dispersal ability, in species that are shifting their ranges could be relevant in this context. Furthermore, trans-generational studies on butterflies could have a great impact on our understanding of the importance of trans-generational effects in wild populations.

Some of the underlying mechanisms of parental effects are nowadays better understood but we still lack information on many aspects. We know, for example, that hormones can mediate between environment and gene expression, and therefore represent molecules that have a role in epigenetics and in turn in maternal effects (Gilbert 2005). It has been widely accepted that epigenetic mechanisms including DNA methylation represent another layer of genome regulation that can increase the flexibility of the organism resulting in phenotypic plasticity (Suzuki and Bird 2008; Foret et al. 2009). DNA methylation in insects compared to vertebrates is sparse (Lyko et al. 2010; Xiang et al. 2010) and represents next to the generally small genomes and short life span another reason why the focus of DNA methylation in the context of environmentally induced phenotypic plasticity has become of high interest in insects (reviewed by Glastad et al. 2011; Lyko and Maleszka 2011). Nevertheless, the mechanism how the environment can be linked to the genome and by what factors epigenomic settings can be adjusted is not yet fully understood. As far as we know, the mechanisms underlying trans-generational effects in Lepidoptera have not really been studied. Hopefully, we will see a change in this in near future as more sequenced genomes are becoming available in Lepidoptera.

Understanding the role of trans-generational effects in shaping life histories of Lepidoptera is also becoming more relevant with the ongoing global change. Changes in climatic conditions and in habitat quality are likely to impact a number of species in nature. Even though parental effects may represent a source of rapid adaptive response, as they can increase offspring fitness in the case of abrupt environmental changes or stressful events (Mousseau and Fox 1998; Marshall and Uller 2007; Coslovsky and Richner 2011), it may also be that in the future it is going to be more difficult for the parents to predict the conditions that their offspring will be facing with, potentially causing mismatch between the predicted and optimal phenotype of the offspring. The impact of such mismatch can only be predicted with a better understanding of the adaptive significance of both maternal and paternal effects in the ecologically well-understood species of Lepidoptera.

## Funding

This work was supported by funding from the Academy of Finland (Decision numbers 273098 and 265641 to MS) and the European Research Council (Independent Starting grant META-STRESS; 637412) to MS.



## Acknowledgments

This review is one of the outcome articles related to the symposia on ‘the evolution of phenotypic plasticity’ at ESEB 2015 meeting (organized by Matthew Walsh and Steve Munch). We would like to thank Steven Parratt and Kristjan Niitepõld as well as 2 anonymous referees for their comments, which have substantially improved the manuscript.

## Supplementary Material

Supplementary material can be found at <http://www.cz.oxfordjournals.org/>.

## References

- Agrawal AA, 2002. Herbivory and maternal effects: mechanisms and consequences of transgenerational induced plant resistance. *Ecology* 83: 3408–3415.
- Agrawal AA, Laforsch C, Tollrian R, 1999. Transgenerational induction of defences in animals and plants. *Nature* 401: 60–63.
- Atkinson D, Morley SA, Hugher RN, 2006. From cells to colonies: at what levels of body organization does the ‘temperature - size rule’ apply? *Evol Dev* 8: 202–214.
- Baguette M, Schtickzelle N, 2006. Negative relationship between dispersal distance and demography in butterfly metapopulations. *Ecology* 87: 648–654.
- Bauerfeind SS, Fischer K, 2005. Effects of food stress and density in different life stages on reproduction in a butterfly. *Oikos* 111: 514–524.
- Bauerfeind SS, Fischer K, Hartstein S, Janowitz S, Martin-Creutzburg D, 2007. Effects of adult nutrition on female reproduction in a fruit-feeding butterfly: the role of fruit decay and dietary lipids. *J Insect Physiol* 53: 964–973.
- Beldade P, Brakefield PM, 2002. The genetics and evo-devo of butterfly wing patterns. *Nat Rev Genet* 3: 442–452.
- Benton TG, St Clair JJ, Plaistow SJ, 2008. Maternal effects mediated by maternal age: from life histories to population dynamics. *J Anim Ecol* 77: 1038–1046.
- Bernardo J, 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am Zool* 36: 216–236.
- Boggs CL, 1997. Reproductive allocation from reserves and income in butterfly species with differing adult diets. *Ecology* 78: 181–191.
- Boggs CL, Gilbert LE, 1979. Male contribution to egg production in butterflies: evidence for transfer of nutrients at mating. *Science* 206: 83–84.
- Boggs CL, Ross CL, 1993. The effect of adult food limitation on life history traits in *Speyeria mormonia*. *Ecology* 74: 433–441.
- Boggs CL, Freeman KD, 2005. Larval food limitation in butterflies: effects on adult resource allocation and fitness. *Oecologia* 144: 353–361.
- Boggs CL, Niitepõld K, 2014. Insights from stable isotopic tracers on reproductive allocation under stress. *Integr Comp Biol* 54: 880–889.
- Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M et al., 2012. Costs of dispersal. *Biol Rev Camb Philos Soc* 87: 290–312.
- Brakefield PM, Reitsma N, 1991. Phenotypic plasticity, seasonal climate and the population biology of *Bicyclus* butterflies (Satyridae) in Malawi. *Ecol Entomol* 16: 291–303.
- Brakefield PM, French V, 1993. Butterfly wing patterns: developmental mechanisms and evolutionary change. *Acta Biotheoretica* 41: 447–468.
- Brakefield PM, Kesbeke F, Koch PB, 1998. The regulation of phenotypic plasticity of eyespots in the butterfly *Bicyclus anynana*. *Am Nat* 152: 853–860.
- Cahenzli F, Erhardt A, 2012. Enhancing offspring quality or quantity? Different ways for using nectar amino acids in female butterflies. *Oecologia* 169: 1005–1014.
- Cahenzli F, Erhardt A, 2013a. Nectar amino acids enhance reproduction in male butterflies. *Oecologia* 171: 197–205.
- Cahenzli F, Erhardt A, 2013b. Transgenerational acclimatization in an herbivore - host plant relationship. *Proc R Soc B* 280: 20122856.
- Cahenzli F, Wenk B, Erhardt A, 2015. Female butterflies adapt and allocate their progeny to the host - plant quality of their own larval experience. *Ecology* 96: 1966–1973.
- Campbell RW, 1963a. The role of disease and desiccation in the population dynamics of the gypsy moth *Porthetria dispar* (L.) (Lepidoptera: Lymantriidae). *Can Entomol* 95: 426–434.
- Campbell RW, 1963b. Some factors that distort the sex ratio of the gypsy moth *Porthetria dispar* (L.) (Lepidoptera: Lymantriidae). *Can Entomol* 95: 465–474.
- Carisey N, Bauce É, 2002. Does nutrition-related stress carry over to spruce budworm *Choristoneura fumiferana* (Lepidoptera: Tortricidae) progeny? *Bull Entomol Res* 92: 101–108.
- Chew FS, Robbins RK, 1984. *Egg-laying in Butterflies*. Princeton (NJ): Princeton University Press.
- Coslovsky M, Richner H, 2011. Predation risk affects offspring growth via maternal effects. *Funct Ecol* 25: 878–888.
- Courtney SP, 1981. Coevolution of pierid butterflies and their cruciferous foodplants. III. *Anthocharis cardamines* (L.) survival, development and oviposition on different hostplants. *Oecologia* 51: 91–96.
- De Roode JC, Gold LR, Altizer S, 2007. Virulence determinants in a natural butterfly - parasite system. *Parasitol* 134: 657–668.
- Ducatez S, Baguette M, Stevens VM, Legrand D, Freville H, 2012. Complex interactions between paternal and maternal effects: parental experience and age at reproduction affect fecundity and offspring performance in a butterfly. *Evolution* 66: 3558–3569.
- Erelli MC, Elkinton JS, 2000. Maternal effects on gypsy moth (Lepidoptera: Lymantriidae) population dynamics: a field experiment. *Env Entomol* 29: 476–488.
- Fischer K, Brakefield PM, Zwaan BJ, 2003a. Plasticity in butterfly egg size: why larger offspring at lower temperatures? *Ecology* 84: 3138–3147.
- Fischer K, Eenhoorn E, Bot AN, Brakefield PM, Zwaan BJ, 2003b. Cooler butterflies lay larger eggs: developmental plasticity versus acclimation. *Proc Biol Sci* 270: 2051–2056.
- Foret S, Kucharski R, Pittelkow Y, Lockett GA, Maleszka R, 2009. Epigenetic regulation of the honey bee transcriptome: unravelling the nature of methylated genes. *BMC Genomics* 10: 472.
- Freitag D, Heckel DG, Vogel H, 2009. Dietary-dependent trans-generational immune priming in an insect herbivore. *Proc Biol Sci* 276: 2617–2624.
- Friberg M, Karlsson B, 2010. Life-history polyphenism in the map butterfly *Araschnia levana*: developmental constraints versus season-specific adaptations. *Evol Ecol Res* 12: 603–615.
- Geister TL, Lorenz MW, Hoffmann KH, Fischer K, 2008. Adult nutrition and butterfly fitness: effects of diet quality on reproductive output, egg composition, and egg hatching success. *Front Zool* 5: 10.
- Geister TL, Lorenz MW, Hoffmann KH, Fischer K, 2009. Energetics of embryonic development: effects of temperature on egg and hatchling composition in a butterfly. *J Comp Physiol B* 179: 87–98.
- Gibbs M, Breuker CJ, Van Dyck H, 2010a. Flight during oviposition reduces maternal egg provisioning and influences offspring development in *Pararge aegeria* (L.). *Physiol Entomol* 35: 29–39.
- Gibbs M, Van Dyck H, Karlsson B, 2010b. Reproductive plasticity, ovarian dynamics and maternal effects in response to temperature and flight in *Pararge aegeria*. *J Insect Physiol* 56: 1275–1283.
- Gibbs M, Breuker CJ, Hesketh H, Hails RS, Van Dyck H, 2010c. Maternal effects, flight versus fecundity trade-offs, and offspring immune defence in the speckled wood butterfly *Pararge aegeria*. *BMC Evol Biol* 10: 345.
- Gibbs M, Van Dyck H, Breuker CJ, 2012. Development on drought-stressed host plants affects life-history, flight morphology and reproductive output relative to landscape structure. *Evol Appl* 5: 66–75.
- Giesel JT, 1986. Effects of parental photoperiod regime on progeny development time in *Drosophila simulans*. *Evolution* 40: 649–651.
- Gilbert SF, 2005. Mechanisms for the environmental regulation of gene expression: Ecological aspects of animal development. *J Biosci* 30: 65–74.
- Glastad KM, Hunt BG, Yi SV, Goodisman MA, 2011. DNA methylation in insects: on the brink of the epigenomic era. *Insect Mol Biol* 20: 553–565.
- Gluckman PD, Hanson MA, Spencer HG, 2005. Predictive adaptive responses and human evolution. *Trends Ecol Evol* 20: 527–533.

- Gotthard K, Nylin S, Wiklund C, 1994. Adaptive variation in growth rate: life-history costs and consequences in the speckled wood butterfly, *Pararge aegeria*. *Oecologia* 99: 281–289.
- Gould F, 1988. Stress specificity of maternal effects in *Heliothis virescens* (boddie)(Lepidoptera: Noctuidae) larvae. *Mem Entomol Soc Can* 120: 191–197.
- Gwynne DT, 1988. Courtship feeding and the fitness of female katydids (Orthoptera: Tettigoniidae). *Evolution* 42: 545–555.
- Hanski I, Saastamoinen M, Ovaskainen O, 2006. Dispersal-related life-history trade-offs in a butterfly. *J Anim Ecol* 75: 91–100.
- Hill JK, Griffiths HM, Thomas CD, 2011. Climate change and evolutionary adaptations at species' range margins. *Annu Rev Entomol* 56: 143–159.
- Henniges-Janssen K, Reineke A, Heckel DG, Groot AT, 2011. Complex inheritance of larval adaptation in *Plutella xylostella* to a novel host plant. *Heredity (Edinb)* 107: 421–432.
- Hunt J, Simmons LW, 1998. Patterns of parental provisioning covary with male morphology in a horned beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Behav Ecol Sociobiol* 42: 447–451.
- Janowitz SA, Fischer K, 2011. Opposing effects of heat stress on male versus female reproductive success in *Bicyclus anynana* butterflies. *J Therm Biol* 36: 283–287.
- Kaitala A, Wiklund C, 1995. Female mate choice and mating costs in the polyandrous butterfly *Pieris napi* (Lepidoptera: Pieridae). *J Insect Behav* 8: 355–363.
- Karl I, Lorenz MW, Fischer K, 2007. Energetics of reproduction: consequences of divergent selection on egg size, food limitation, and female age for egg composition and reproductive effort in a butterfly. *Biol J Linn Soc* 91: 403–418.
- Karlsson B, Stjernholm F, Wiklund C, 2008. Test of a developmental trade-off in a polyphenic butterfly: direct development favours reproductive output. *Funct Ecol* 22: 121–126.
- Keena MA, Odell TM, Tanner JA, 1998. Environmentally based maternal effects are the primary factor in determining the developmental response of gypsy moth (Lepidoptera: Lymantriidae) to dietary iron deficiency. *Ann Entomol Soc Am* 91: 710–718.
- Kehl T, Beaulieu M, Kehl A, Fischer K, 2015. Old male sex: large ejaculate, many sperm, but few offspring. *Behav Ecol Sociobiol* 69: 1543–1552.
- Kingsolver JG, Wiernasz DC, 1991. Seasonal polyphenism in wing - melanin pattern and thermoregulatory adaptation in *Pieris* butterflies. *Am Nat* 137: 816–830.
- Klein J, 1989. Are invertebrates capable of an anticipatory immune responses? *Scand J Immunol* 29(5): 499–505.
- Kong H, Cheng Y, Luo L, Sappington TW, Jiang X, Zhang L, 2013. Density-dependent prophylaxis in crowded Beet webworm *Loxostege sticticalis* (Lepidoptera: Pyralidae) larvae to a parasitoid and a fungal pathogen. *Int J Pest Manag* 59: 174–179.
- Kuussaari M, Singer MC, Hanski I, 2000. Local specialization and landscape-level influence on host use in an herbivorous insect. *Ecology* 81: 2177–2187.
- Krug PJ, Zimmer RK, 2000. Developmental dimorphism and expression of chemosensory-mediated behaviour: habitat selection by a specialist marine herbivore. *J Exp Biol* 203: 1741–1754.
- Krug PJ, 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. *Mar Ecol Prog Ser* 213: 177–192.
- Ladner DT, Altizer S, 2005. Oviposition preference and larval performance of North American monarch butterflies on four *Asclepias* species. *Entomol Exp et Appl* 116: 9–20.
- Leimar O, McNamara JM, 2015. The Evolution of transgenerational integration of information in heterogeneous environments. *Am Nat* 185: E55–E69.
- Little TJ, O'Connor B, Colegrave N, Watt K, Read AF, 2003. Maternal transfer of strain-specific immunity in an invertebrate. *Curr Biol* 13: 489–492.
- Lyko F, Maleszka R, 2011. Insects as innovative models for functional studies of DNA methylation. *Trends Genet* 27: 127–131.
- Lyko F, Foret S, Kucharski R, Wolf S, Falckenhayn C et al., 2010. The honey bee epigenomes: differential methylation of brain DNA in queens and workers. *PLoS Biol* 8: e1000506.
- Marshall DJ, Uller T, 2007. When is a maternal effect adaptive? *Oikos* 116: 1957–1963.
- Mattila ALK, Hanski I, 2014. Heritability of flight and resting metabolic rates in the *Glanville fritillary* butterfly. *J Evol Biol* 27: 1733–1743.
- Mayhew PJ, 2001. Herbivore host choice and optimal bad motherhood. *Trends Ecol Evol* 16: 165–167.
- Mevi-Schütz J, Erhardt A, 2003. Effects of nectar amino acids on fecundity of the wall brown butterfly (*Lasiommata megera* L.). *Basic Appl Ecol* 4: 413–421.
- Mironidis GK, Savopoulou-Soultani M, 2010. Effects of heat shock on survival and reproduction of *Helicoverpa armigera* (Lepidoptera: Noctuidae) adults. *J Therm Biol* 35: 59–69.
- Moran NA, 1992. The Evolutionary maintenance of alternative phenotypes. *Am Nat* 139: 971–989.
- Moret Y, 2006. "Trans-generational immune priming": specific enhancement of the antimicrobial immune response in the mealworm beetle *Tenebrio molitor*. *Proc Biol Sci* 273: 1399–1405.
- Morris RF, 1967. Influence of parental food quality on the survival of *Hyphantria cunea*. *Can Entomol* 99: 24–33.
- Mousseau TA, Dingle H, 1991. Maternal effects in insect life histories. *Annu Rev Entomol* 36: 511–534.
- Mousseau TA, Fox CW, 1998. The adaptive significance of maternal effects. *Trends Ecol Evol* 13: 403–407.
- Murphy SM, Loewy KJ, 2015. Trade-offs in host choice of an herbivorous insect based on parasitism and larval performance. *Oecologia* 179: 741–751.
- Myers JH, Boettner G, Elkinton J, 1998. Maternal effects in gypsy moth: only sex ratio varies with population density. *Ecology* 79: 305–314.
- Myers JH, Cory JS, Ericsson JD, Tseng ML, 2011. The effect of food limitation on immunity factors and disease resistance in the western tent caterpillar. *Oecologia* 167: 647–655.
- Niitepöld K, Perez A, Boggs CL, 2014. Aging, life span, and energetics under adult dietary restriction in Lepidoptera. *Physiol Biochem Zool* 87: 684–694.
- Nylin S, 1992. Seasonal plasticity in life-history traits: growth and development in *Polygona c-album* (Lepidoptera: Nymphalidae). *Biol J Linn Soc* 47: 301–323.
- Nylin S, Gotthard K, 1998. Plasticity in life-history traits. *Annu Rev Entomol* 43: 63–83.
- Oberhauser KS, 1997. Fecundity, lifespan and egg mass in butterflies: effects of male-derived nutrients and female size. *Funct Ecol* 11: 166–175.
- Oostra V, de Jong MA, Invergo BM, Kesbeke F, Wende F et al., 2011. Translating environmental gradients into discontinuous reaction norms via hormone signalling in a polyphenic butterfly. *Proc Biol Sci* 278: 789–797.
- Pembrey ME, Bygren LO, Kaati G, Edvinsson S, Northstone K et al., 2006. Sex-specific, male-line transgenerational responses in humans. *Eur J Hum Genet* 14: 159–166.
- Pham LN, Schneider DS, 2008. Evidence for specificity and memory in the insect innate immune response. In: Beckage EN, editor. *Insect Immunology*. Heidelberg: Academic Press. 97–127.
- Piesk M, Karl I, Franke K, Fischer K, 2013. High larval density does not induce a prophylactic immune response in a butterfly. *Ecol Entomol* 38: 346–354.
- Pijpe J, Brakefield PM, Zwaan BJ, 2007. Phenotypic plasticity of starvation resistance in the butterfly *Bicyclus anynana*. *Evol Ecol* 21: 589–600.
- Pijpe J, Fischer K, Brakefield PM, Zwaan BJ, 2006. Consequences of artificial selection on pre-adult development for adult lifespan under benign conditions in the butterfly *Bicyclus anynana*. *Mech Ageing Dev* 127: 802–807.
- Priest NK, Roach DA, Galloway LF, 2008. Cross-generational fitness benefits of mating and male seminal fluid. *Biol Lett* 4: 6–8.
- Refsnider JM, Janzen FJ, 2010. Putting eggs in one basket: ecological and evolutionary hypotheses for variation in oviposition-site choice. *Annu Rev Ecol Evol Syst* 41: 39–57.
- Resetarits WJ, 1996. Oviposition site choice and life-history evolution. *Am Zool* 36: 205–215.

- Rickard IJ, Lummaa V, 2007. The predictive adaptive response and metabolic syndrome: challenges for the hypothesis. *Trends Endocrinol Metab* 18(3): 94–99.
- Rossiter MC, 1991. Environmentally-based maternal effects: a hidden force in insect population dynamics? *Oecologia* 87: 288–294.
- Rossiter MC, Cox-Foster DL, Briggs MA, 1993. Initiation of maternal effects in *Lymantria dispar*: genetic and ecological component of egg provisioning. *J Evol Biol* 6: 577–589.
- Rotem K, Agrawal AA, Kott L, 2003. Parental effects in *Pieris rapae* in response to variation in food quality: adaptive plasticity across generations? *Ecol Entomol* 28: 211–218.
- Roth O, Joop G, Eggert H, Hilbert J, Daniel J et al., 2010. Paternally derived immune priming for offspring in the red flour beetle *Tribolium castaneum*. *J Anim Ecol* 79: 403–413.
- Rothman LD, 1997. Immediate and delayed effects of a viral pathogen and density on tent caterpillar performance. *Ecology* 78: 1481–1493.
- Saastamoinen M, Hirai N, van Nouhuys S, 2013a. Direct and trans-generational responses to food deprivation during development in the Glanville fritillary butterfly. *Oecologia* 171: 93–104.
- Saastamoinen M, Brommer JE, Brakefield PM, Zwaan BJ, 2013b. Quantitative genetic analysis of responses to larval food limitation in a polyphenic butterfly indicates environment- and trait- specific effects. *Ecol Evol* 3: 3576–3589.
- Saastamoinen M, van der Sterren D, Vastenhout N, Zwaan BJ, Brakefield PM, 2010. Predictive adaptive responses: condition-dependent impact of adult nutrition and flight in the tropical butterfly *Bicyclus anynana*. *Am Nat* 176: 686–698.
- Sadd BM, Schmid-Hempel P, 2008. PERSPECTIVE: principles of ecological immunology. *Evol Appl* 2: 113–121.
- Sakamoto Y, Hirai N, Ishii M, 2015. Effects of photoperiod and temperature on the development and diapause of the endangered butterfly *Zizina emelina* (Lepidoptera: Lycaenidae). *J Insect Conserv* 19: 639–645.
- Saunders DS, 1966. Larval diapause of maternal origin—II. The effect of photoperiod and temperature on *Nasonia vitripennis*. *J Insect Phys* 12: 569–581.
- Schoonhoven LM, Beerling EAM, Klijnstra JW, van Vugt Y, 1990. Two related butterfly species avoid oviposition near each other's eggs. *Experientia* 46: 526–528.
- Simmons LW, 1990. Nuptial feeding in tettigoniids male costs and the rates of fecundity increase. *Behav Ecol Sociobiol* 27: 43–47.
- Steigenga MJ, Fischer K, 2007. Within- and between- generation effects of temperature on life-history traits in a butterfly. *J Therm Biol* 32: 396–405.
- Sternberg ED, de Roode JC, Hunter MD, 2015. Trans-generational parasite protection associated with paternal diet. *J Anim Ecol* 84: 310–321.
- Suzuki MM, Bird A, 2008. DNA methylation landscapes: provocative insights from epigenomics. *Nat Rev Genet* 9: 465–476.
- Svärd L, Wiklund C, 1989. Mass and production rate of ejaculates in relation to monandry/polyandry in butterflies. *Behav Ecol Sociobiol* 24: 395–402.
- Talloe W, Van Dyck H, Lens L, 2004. The cost of melanization: butterfly wing coloration under environmental stress. *Evol Dev* 58: 360–366.
- Tarin JJ, Gomez-Piquer V, Rausell F, Navarro S, Hermenegildo C et al., 2005. Delayed motherhood decreases life expectancy of mouse offspring. *Biol Reprod* 72: 1336–1343.
- Thompson JN, Pellmyr O, 1991. Evolution of oviposition behaviour and host preference in Lepidoptera. *Annu Rev Entomol* 36: 65–89.
- Tidbury HJ, Pedersen AB, Boots M, 2011. Within and transgenerational immune priming in an insect to a DNA virus. *Proc Biol Sci* 278: 871–876.
- Triggs A, Knell RJ, 2012. Interactions between environmental variables determine immunity in the Indian meal moth *Plodia interpunctella*. *J Anim Ecol* 81: 386–394.
- Uller T, 2008. Developmental plasticity and the evolution of parental effects. *Trends Ecol Evol* 23: 432–438.
- van Asch M, Julkunen-Tiito R, Visser ME, 2010. Maternal effects in an insect herbivore as a mechanism to adapt to host plant phenology. *Funct Ecol* 24: 1103–1109.
- van den Heuvel J, Saastamoinen M, Brakefield PM, Kirkwood TBL, Zwaan BJ et al., 2013. The predictive adaptive response: modeling the life-history evolution of the butterfly *Bicyclus anynana* in seasonal environments. *Am Nat* 181: E28–E42.
- Van Dyck H, Wiklund C, 2002. Seasonal butterfly design: morphological plasticity among three developmental pathways relative to sex, flight and thermoregulation. *J Evol Biol* 15: 216–225.
- Van Nouhuys S, Singer MC, Nieminen M, 2003. Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. *Ecol Entomol* 28: 193–202.
- Venturelli PA, Murphy CA, Shuter BJ, Johnston TA, van Coeverden de Groot PJ et al., 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. *Ecology* 91: 2003–2012.
- Wedell N, Karlsson B, 2003. Paternal investment directly affects female reproductive effort in an insect. *Proc R Soc Lond B* 270: 2065–2071.
- Wiklund C, Forsberg J. 1991. Sexual size dimorphism in relation to female polygamy and protandry in butterflies: a comparative study of Swedish Pieridae and Satyridae. *Oikos* 60: 373–381
- Wiklund C, Kaitala A, Lindfors V, Abenius J, 1993. Polyandry and its effect on female reproduction in the green-veined white butterfly (*Pieris napi* L.). *Behav Ecol Sociobiol* 33: 25–33.
- Wiklund C, Persson A, 1983. Fecundity, and the Relation of Egg Weight Variation to Offspring Fitness in the Speckled Wood Butterfly *Pararge aegeria*, or Why Don't Butterfly Females Lay More Eggs? *Oikos* 40(1):53–63.
- Xiang H, Zhu JD, Chen Q, Dai FY, Li X et al., 2010. Single base-resolution methylome of the silkworm reveals a sparse epigenomic map. *Nat Biotechnol* 28: 516–520.
- Zanchi C, Troussard JP, Martinaud G, Moreau J, Moret Y, 2011. Differential expression and costs between maternally and paternally derived immune priming for offspring in an insect. *J Anim Ecol* 80: 1174–1183.
- Zhang W, Zhao F, Hoffmann AA, Ma C-S, 2013. A single hot event that does not affect survival but decreases reproduction in the diamondback moth *Plutella xylostella*. *PLoS One* 8.