The importance of trans-generational effects in Lepidoptera

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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; Relsnider 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 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.
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; Niitepold 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 Niitepold 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                                           |
|---------------------------|-----------|--------------------------------|-----------------------------------------------------|
| **Abiotic**               |           |                                |                                                     |
| High temperature          | ↓         | Egg fertility                  | Helicoverpa armigera                                 | Mironidis and Savopoulou-Soutiani (2010) |
|                           | ↓         | Egg mass                       | Bicyclus anynana                                    | Janowitz and Fischer (2011)               |
|                           | ↓         | Egg size                       | Bicyclus anynana                                    | Janowitz and Fischer (2011)               |
|                           | ↑         | Hatching success               | Plutella xylostella                                 | Zhang et al. (2013)                       |
|                           | ↑         |                                | Bicyclus anynana                                    | Janowitz and Fischer (2011)               |
|                           |           | Egg size                       | Bicyclus anynana                                    | Geister et al. (2009)                     |
|                           |           |                                | Pararge aegeria                                      | Fischer et al. (2003b); Geister et al. (2009) |
|                           | ↓         | Egg mass                       | Pararge aegeria                                      | Geister et al. (2009)                     |
|                           | ↑         | Egg size                       | Pararge aegeria                                      | Geister et al. (2009)                     |
| Low temperature           |           | Egg composition                | Bicyclus anynana                                    | Geister et al. (2009)                     |
|                           |           |                                | Pararge aegeria                                      | Geister et al. (2009)                     |
|                           | ↑         | Egg mass                       | Pararge aegeria                                      | Geister et al. (2009)                     |
|                           |           | Egg size                       | Pararge aegeria                                      | Geister et al. (2009)                     |
| Biotic                    |           | C/N ratio                      | Lasiommata megera                                   | Mevi-Schütz and Erhardt (2003)            |
| Good food quality         |           | Egg composition                | Bicyclus anynana                                    | Karl et al. (2007); Geister et al. (2008) |
|                           |           |                                | Lyantria dispar                                      | Rossiter et al. (1993)                    |
|                           |           | Egg developmental time         | Coenonympha pamphilus                               | Cahanzli and Erhardt (2013a)              |
|                           |           | Egg size                       | Bicyclus anynana                                    | Bauerfeind et al. (2007)                  |
|                           |           | Egg mass                       | Choristoneura fimiferana                             | Carisey and Bauce (2002)                  |
|                           |           |                                | Lymantria dispar                                     | Rossiter et al. (1993)                    |
|                           |           | Hatching success               | Hyphantria cunea, Bicyclus anynana                  | Morris (1967); Geister et al. (2008); Cahanzli and Erhardt (2012) |
| Poor food quality         |           | C/N ratio                      | Lasiommata megera                                   | Mevi-Schütz and Erhardt (2003); Cahanzli and Erhardt (2013a) |
|                           |           | Egg composition                | Bicyclus anynana                                    | Karl et al. (2007); Geister et al. (2008) |
|                           |           |                                | Lyantria dispar                                      | Rossiter et al. (1993)                    |
|                           |           | Egg developmental time         | Coenonympha pamphilus                               | Cahanzli and Erhardt (2013a)              |
|                           |           | Egg size                       | Bicyclus anynana                                    | Bauerfeind et al. (2007)                  |
|                           |           | Egg mass                       | Choristoneura fimiferana                             | Carisey and Bauce (2002)                  |
|                           |           |                                | Lymantria dispar                                     | Rossiter et al. (1993)                    |
|                           |           | Offspring weight               | Lasiommata megera                                   | Mevi-Schütz and Erhardt (2003); Geister et al. (2008) |
|                           |           | Immunity                       | Malacosoma pluviale californicum                     | Myers et al. (2011)                      |
|                           |           | Female/male sex-ratio          | Melitaea cinxia                                      | Saastamoinen et al. (2013a)               |
|                           |           |                                | Danaus plexippus                                    | Sternberg et al. (2015)                   |
|                           |           | Offspring survival             | Lymantria dispar                                     | Ereli and Elkinton (2000)                 |
|                           |           |                                | Hyphantria cunea                                     | Morris (1967)                            |
|                           |           | Offspring survival             | Lasiommata megera, Bicyclus anynana                 | Mevi-Schütz and Erhardt (2003); Geister et al. (2008) |
|                           |           | Immunity                       | Melitaea cinxia                                      | Saastamoinen et al. (2013a)               |
|                           |           |                                | Danaus plexippus                                    | Sternberg et al. (2015)                   |
|                           |           | Offspring survival             | Choristoneura fimiferana                             | Carisey and Bauce (2002); Bauerfeind et al. (2007) |
|                           |           | Offspring survival             | Lymantria dispar                                     | Ereli and Elkinton (2000)                 |
|                           |           | Offspring size                 | Ploidia interpunctella                               | Triggs and Knell (2012)                   |
|                           |           |                                | Erythrina dispar                                     | Keena et al. (1998)                      |
|                           |           | Offspring survival             | Choristoneura fimiferana                             | Carisey and Bauce (2002); Saastamoinen et al. (2013a) |
|                           |           | Offspring size                 | Melitaea cinxia                                      | Saastamoinen et al. (2013a)               |
|                           |           |                                | Danaus plexippus                                    | Rotem et al. (2003)                      |
|                           |           | Offspring survival             | Choristoneura fimiferana                             | Carisey and Bauce (2002); Saastamoinen et al. (2013a) |
|                           |           | Offspring size                 | Melitaea cinxia                                      | Saastamoinen et al. (2013a)               |
|                           |           |                                | Danaus plexippus                                    | Rotem et al. (2003)                      |

(continued)
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

| Trait affected                  | Direction | Species                  | References                                      |
|---------------------------------|-----------|--------------------------|-------------------------------------------------|
| Pupal mass                      | ↑         | Lymantria dispar         | Rossiter (1991)                                 |
| Offspring performance           | ↑         | Pieris rapae             | Czarny et al. (2015)                             |
| Developmental time              | ↑         | Coenonympha pamphilus    | Czarny and Erhardt (2013b)                       |
| Tolerance to starvation         | ↑         | Choristoneura fumiferana | Czarny and Erhardt (2002)                        |
| Forewing size                   | ↑         | Pararge aegeria          | Czarny and Erhardt (2013b)                       |
| Egg fertility                   | ↓         | Pararge aegeria          | Wiklund and Persson (1983)                       |
| Egg size                        | ↓         | Lasiomma magera          | Wiklund and Persson (1983); Myers et al. (2003) |
| Egg survival until adult emergence | ↓       | Pieris brassicae        | Ducatez et al. (2012)                            |
| Egg mass                        | ↓         | Lasiomma magera, Pararge aegeria | Mevi-Schütz and Erhardt (2003); Gibbs et al. (2010b) |
| Embryonic developmental time    | ↑         | Pararge aegeria          | Gibbs et al. (2010c)                             |
| Hatching success                | ↓         | Bicyclus arynana         | Bauerfeind et al. (2007)                         |
| Larval mass                     | ↓         | Bicyclus arynana         | Kehl et al. (2015)                               |
| Offspring adult life span       | ↓         | Pararge aegeria          | Gibbs et al. (2010c)                             |
| Sperm number                    | ↑         | Bicyclus arynana         | Kehl et al. (2015)                               |
| Spermatophore mass              | ↑         | Bicyclus arynana         | Kehl et al. (2015)                               |
| Female/male sex-ratio           | ↑         | Lymantria dispar         | Myers et al. (1998)                              |
| Egg viability                   | –         | Malacosoma pluviale californicum | Rothman (1997)                                  |
| Larval developmental time       | –         | Malacosoma pluviale californicum | Rothman (1997)                                  |
| Mortality                       | –         | Malacosoma pluviale californicum | Rothman (1997)                                  |
| Pupal mass                      | ↑         | Malacosoma pluviale californicum | Rothman (1997)                                  |
| Egg size                        | ↓         | Pararge aegeria          | Gibbs et al. (2010a)                             |
| Egg to pupa survival            | –         | Pararge aegeria          | Gibbs et al. (2010a)                             |
| Hatching success                | ↓         | Pararge aegeria          | Gibbs et al. (2010a)                             |
| Larval developmental time       | ↑         | Pararge aegeria          | Gibbs et al. (2009a, 2010c)                      |
| Larval mass                     | ↓         | Pararge aegeria          | Gibbs et al. (2010c)                             |
| Immunity                        | ↓         | Pararge aegeria          | Gibbs et al. (2010c)                             |
| Flight metabolic rate            | ↑         | Melitaea cinxia          | Mattila and Hanski (2014)                        |
| Resting metabolic rate           | ↓         | Melitaea cinxia          | Mattila and Hanski (2014)                        |
| Developmental time              | ↑         | Trichoplasia ni          | Freitak et al. (2009)                            |
| Immunity                        | ↑         | Trichoplasia ni          | Freitak et al. (2009)                            |
| Susceptibility to viral exposure | ↓         | Plodia interpunctella    | Tubdy et al. (2011)                              |
| Mortality                       | ↑         | Trichoplasia ni          | Freitak et al. (2009)                            |
| Egg mass                        | ↑         | Pieris napi              | Wiklund and Karlsson (1993)                      |
| Reproductive effort             | –         | Pararge aegeria          | Wedell and Karlsson (2003)                       |
| Egg mass                        | ↑         | Pararge aegeria          | Wedell and Karlsson (2003)                       |
| Growth                          | –         | Danaus plexippus         | Ladner and Altizer (2005)                        |
| Oviposition-choice              | –         | Danaus plexippus         | Ladner and Altizer (2005)                        |

[Table 1. Continued]

a Change detected, direction not specified (for details see Supplementary Table 1).
b Animal model study: flight metabolic rate is heritable whereas resting metabolic rate underlies a strong 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 (Resatarits 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. Schoenhoven et al. 1990, Brakefield and French 1993). Oviposition on ideal host plants or ideal microhabitat increases also offspring 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 (Melitaea cinxia) uses two hosts: Plantago lanceolata and Veronica spicata (Fig. 2). This butterfly evolves local adaption 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).
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; Carney and Bause 2002), starvation during development (M. cinxia; Saastamoinen et al. 2013a), plant defense components (H. virescens; Gould 1988), or amounts of protein in the diet (P. 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 spermato- phores 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 spermaphore 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 spermaphore size and composition (Svärd and Wiklund 1989; Wiklund and Forsberg 1991). Already mated males produce a smaller second spermaphore, 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 spermaphore 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 spermaphore quality that in turn influenced offspring quality. However, spermaphore 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 P. 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;
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 bactericidal 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 Maleksza 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.

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

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