Transgenerational effect of host plant on growth and reproduction in two species of moth, Cacoecimorpha pronubana and Epiphyas postvittana (Lepidoptera: Tortricidae)

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Transgenerational effect of host plant on growth and reproduction in two species of moth, *Cacoecimorpha pronubana* and *Epiphyas postvittana* (Lepidoptera: Tortricidae)

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Abstract

The carnation tortrix moth, *Cacoecimorpha pronubana* (Roelofs & Brown, 1982), and the light brown apple moth, *Epiphyas postvittana* (Walker, 1863) (Lepidoptera: Tortricidae) are two important polyphagous pest species affecting a wide range of plant species many of which are horticultural crops. Crop damage is caused by the larvae of these two moths rolling leaves together and feeding on the foliage. In order to understand how these two species are affected by a host plant through transgenerational dietary changes, we hypothesised that larval parental pre-treatment diet affects growth and reproduction of offspring. We tested the performance of developmental traits of *C. pronubana* and *E. postvittana* on three host plant species (larval diet treatment) – *Prunus* (Rosaceae), *Choisya* (Rutaceae) and *Griselinia* (Griseliniaceae). For the experiment we used larvae from a second generation of *C. pronubana* and *E. postvittana* reared either exclusively on *Prunus*, or reared exclusively on *Griselinia* (pre-treatment). Regardless of whether moths had been reared on *Prunus* or *Griselinia* both species of host plant had a significant average effect on the duration of larval development and the pupal size of both species of moth, for *E. postvittana*, and for *C. pronubana*. Although, neither pre-treatment, nor treatment

had a significant overall effect on fecundity (number of eggs per clutch laid) in either species of moth, there was a significant interaction effect observed between the pre- and post-treatment on fecundity for both species of moth. Our results suggest that changes of host plant species composition can affect the performance of offspring of both these polyphagous pest species intergenerationally in complex ways which are relevant to agroecosystems. Such phenomena may be important when developing new strategies for the integrated pest management of these two important pest species.

Keywords

Herbivory, parental diet, maternal diet, larval diet, larvae, pupae, size, development, fecundity, integrated pest management.

1 | Introduction

The carnation tortrix moth (CTM), *C. pronubana* (Lepidoptera: Tortricidae) (Roelofs & Brown, 1982) and the light brown apple moth (LBAM), *E. postvittana* (Lepidoptera: Tortricidae), (Walker, 1863) are important polyphagous pest species affecting together over 500 plant genera (Kaçar & Ulusoy, 2008; Brockerhoff *et al*., 2011; Pencheva & Yovkova, 2016; Reddy, 2016). Both moth species affect a wide range of woody and herbaceous plants, including many economically important horticultural crops (Fisher, 1924; Brown *et al*., 2010; Suckling & Brockerhoff, 2010). The moths have been present in Britain since at least 1905 and 1930, respectively (Fisher, 1924; CABI, 2020; EPPO, 2020).

Damage to the plant is caused by the larva that feeds on the foliage or fruits. It produces silk and uses it to roll leaves together to protect itself against natural enemies (Fisher, 1924; Bestagno, 1955; Lo *et al*., 2000). Host plants that are known to be a common dietary source for both moth species belong to the families Asteraceae, Fabaceae (CABI, 2020), Griseliniaceae (personal observation), Oleaceae, Rosaceae, Rutaceae and Solanaceae (Beitia *et al*., 2016; CABI, 2020).

The control of these two herbivores often involves the use of synthetic pesticides and there is concern that such pesticides are harmful to the environment and human health (Gaines, 1969; Matos *et al*., 1987; Solomon *et al*., 2001; Stenersen, 2004; Rehman *et al*., 2014; Wang *et al*., 2014; Damalas & Koutroubas, 2016). These two species of Lepidoptera are controlled by natural enemies, such as parasitoids or predators (Cameron, 1912; Kaçar & Ulusoy, 2012; Feng *et al*., 2015a,b; Yazdani, 2015). It has been shown, however, that insecticides (e.g. neonicotinoids and pyrethroids) are harmful to non-target insects, for example, to the parasitoid *Trichogramma evanescens* Westwood, 1833 (Hymenoptera: Trichogramma), which parasitises CTM eggs (Wang *et al*., 2014). In order to reduce the cost and deleterious effects of pesticides in a crop-habitats, many growers consider the adoption of integrated pest management (IPM) practices to control pests (Copping & Menn, 2000; van Lenteren, 2000). This approach, however, relies on

information on both pest life cycles and interactions with the crop habitat (Dhawan & Peshin, 2009). Reproductive performance, for example, may be affected by certain characteristics of the host plant, which are known to influence larval development, pupal size, adult fitness and longevity (Brewer, 1985; Lance, 2012; Moreau *et al*., 2017).

Transgenerational plasticity (TGP), also known as parental environmental effect, occurs when the environment experienced by a parent (through environmental cues) influences the development of their offspring. These can comprise of a wide range of biotic or abiotic factors, e.g. diet, food availability, temperature, toxins, light quality, or immune challenges (Freitak *et al*., 2009; Bell & Hellmann, 2019). TGP may generate, for example, adaptive offspring traits for overcoming specific negative environmental factors (e.g. toxins), but at the same time may reduce overall survival (Kobiela & Snell-Rood, 2018; Bell & Hellmann, 2019). Although, it may consequently promote population persistence in changing environments (Harmon & Pfennig, 2021). This, for example, may have potentially adaptive benefits in the early life stage of an insect (e.g. improving larval survival), although, it may generate fitness costs later in life (e.g. reduced reproductive potential) (Bell & Hellmann, 2019). While TGP is well documented across many taxa, theoretical models are not yet well supported by empirical data (Rösvik *et al*., 2020).

The importance of the effect of host plants on the performance of CTM and LBAM is well documented; it is, however, not known how the performance of these two species of moth is affected by dietary changes through multiple generations for either species. It has been shown, for example, that performance of the African cotton leafworm, *Spodoptera littoralis* (Boisduval, 1833) (Lepidoptera: Noctuidae) offspring can be enhanced through transgenerational phenotypic plasticity on a host plant identical to the parental host plant. However, mechanisms underlying such phenomena are still unknown (Rösvik *et al*., 2020) and basic data are lacking for the majority of pest species.

The main objective of this study was to investigate whether the parental host plant environment during larval development can affect growth and reproduction of offspring transgenerationally.

First, we looked at differences for several traits - survivorship, length of larval and pupal development, pupal and adult weight, sex and fecundity. Specifically, we investigated (i) the average effect of the parental larval diet (pre-treatment), and (ii) the overall effect of the progeny larval diet (treatment) on the growth and reproduction in each of the species of moth. Finally, we tested whether the growth and reproduction of offspring was influenced by the parental diet by analysing (iii) the interaction between larval parental diet (pre-treatment) and progeny larval diet (treatment) for each of the species of moth. This knowledge may be useful in developing more efficient practices within the IPM systems.

2 | Materials and methods

2.1 | Host plants

Plant material was grown and obtained from an ornamental plant nursery in Shropshire, UK (52°37'20'' N, 2°15'20'' W; 119 m a.s.l.). Plants were propagated from softwood cuttings two years before the beginning of the experiment. The cutting material was collected, propagated and grown in black PVC pots (9 cm Ø, 10 cm height) filled with Sinclair® All Purpose Growing Medium Compost (Sinclair Pro, UK) under protected glasshouse conditions. For the maintenance of the stock laboratory moth cultures the following families of host plants were used: Caprifoliaceae, Hypericaceae, Pittosporaceae, Plantaginaceae and Rhamnaceae. For moth cultures used in the experiment the following host plants species were used: *Prunus laurocerasus* var. *schipkaensis* Späth ex H.L.Späth (Rosaceae), *Choisya ternata* Kunth 'Lich' (Rutaceae), and *Griselinia littoralis* Raoul (Griseliniaceae).

2.2 | Insects

Adults of CTM and LBAM were collected in May 2018, from the same ornamental plant nursery from which the host plants were obtained. Two stock laboratory moth cultures were established from these field collected moths in two separate BugDorm-4D® Insect Rearing Cages (47.5 cm × 47.5 cm × 47.5 cm) (MegaView, Taiwan) placed in a Fitotron® SGR plant growth room (Weiss Technik, UK) maintained at a constant temperature 20°C, 60% RH and 16L:8D photoperiod. In September 2018, using larvae collected from the existing two stock laboratory cultures, four new separate moth cultures were initiated - both moth species reared exclusively on *Prunus* (Rosaceae) and separate cultures were reared exclusively on *Griselinia* (Griseliniaceae). As a result, four moth cultures were established: CTM reared on *Prunus* or *Griselinia*, and LBAM reared on *Prunus* or *Griselinia*. Cultures were maintained until two generations on each host plant

had been completed and there was a sufficient number of eggs available to complete the experiment.

2.3 | Experiment

The experiment was set up in February 2019 in a Fitotron® SGR 'Walk-in' plant growth room under the same controlled environmental conditions used to maintain the cultures of CTM and LBAM. The experiment was a randomised block design consisting of two factors, the "pre-treatment" culture (the larval parental diet of either *Griselinia* or *Prunus*) and the "treatment" culture (larval diet of *Prunus, Choisya* or *Griselinia*). Each treatment consisted of six replicates, and the entire experiment was conducted for both moth species. Plants were placed on a black PVC tray and were watered as required from beneath. The height of the plants varied from 20–25 cm, and their mid-width measured approximately 12 cm.

Egg clutches were collected from each of the four pre-experiment cultures and placed separately into Petri dishes (90 mm Ø, 15 mm height) in the same room under the same constant environmental conditions and monitored for hatching larvae. After eggs had hatched, for each replicate five neonate larvae were placed on each experimental plant (towards the top) using a fine paintbrush, after which the plants were covered with a nylon mesh sleeve (13 cm Ø, 43 cm long; mesh aperture 0.17 mm × 0.17 mm, with the open area of a mesh (A^o) = 50%), closed at the top and the bottom in order to isolate plants from each other. Larvae were left undisturbed on each plant to feed and complete their development, and monitored daily to record the time to pupation. Upon pupation, each individual was collected after the integument had hardened and turned brown and weight was recorded. After measurements, pupae were transferred separately to Petri dishes (90 mm Ø, 15 mm height), and placed in a room at a constant temperature 20°C, 60% RH and 16L:8D photoperiod. Each Petri dish had a circular piece of dry plain white paper towel placed on the bottom of the dish.

The weight of each adult was recorded between 6–12 h after emergence from the pupa. Sex was determined by examination under a Microtec HM-3® stereo microscope (TEC Microscopes, UK) and recorded. Each female adult moth was placed into one clear Petri dish and allowed to mate with three introduced unmated males (Knight, 2014) that came from the same host plant species as the female. Each female was allowed to lay eggs on the inside walls of the dish up to its death; during this period eggs were counted every 48h using a Microtec HM-3® stereo microscope, after which eggs were removed.

The following data were recorded for analysis within the experimental design: (1) larval survivorship (the number of larvae out of five surviving until the end of the experiment), (2) the duration of larval development from egg hatching to pupa formation (days), (3) weight of the pupa (mg), (4) the duration of the pupal stage and sex, and (5) fecundity (eggs per clutch) was estimated for female offspring.

2.4 | Statistical analysis

Linear models were used to test for main effects of the pre-treatment (parental diet), treatment (larval diet), and the interaction between parental and larval diet on larval survival (the count of number surviving) per (plant) experimental unit. Linear mixed effects models were used to test for main effects of the pre-treatment (parental diet), treatment (larval diet), the interaction effect between parental and larval diet, and sex on development time and weight for larval and pupal stages, with individual plant as a random effect to account for the measurement of multiple individual insects from each (plant) experimental unit. The data for each moth species were analysed separately. All tests adhered to assumptions of Gaussian residual distribution and homoscedasticity unless otherwise specified. All analyses were performed using R version 4.0.2 (R Core Team, 2020) with $\alpha = 0.05$ using functions in the {nlme} package (Pinheiro *et al*. 2021) and in the base R {stats} package.

3 | Results

Overall mean count of larvae surviving was 70.2%, 3.51 $\pm$ 1.21 (mean $\pm$ 1 SD), and was not significantly different between moth species ($t_{67.8}$ = 1.07, P = 0.29), for CTM at 73.4% (3.67 $\pm$ 1.10) and for LBAM at 67.2% (3.36 $\pm$ 1.31). The larval parental pre-treatment diet had a significant overall effect on LBAM larval survivorship with *Prunus* presenting the highest survivorship (Fig 1A: $F_{1,30}$ = 7.37, P = 0.011), but not for CTM (Fig 1B: $F_{1,30}$ = 2.94, P = 0.097). The larval diet treatment was not significantly different for survivorship for either moth species (LBAM: $F_{2,30}$ = 2.22, P = 0.13; and CTM: $F_{2,30}$ = 2.47, P = 0.10), and neither was the interaction effect between parental and larval diets significant for either species (LBAM: $F_{2,30}$ = 1.24, P = 0.30; CTM: $F_{2,30}$ = 3.29, P = 0.051).

Overall, the mean duration of larval development from egg hatching to pupation was 58.8 $\pm$ 22.6 days, with a significant difference ($F_{1,68.5}$ = 39.15, P < 0.0001) between LBAM (46.0 $\pm$ 13.2 days) and CTM (70.7 $\pm$ 23.0 days). The larval parental pre-treatment diet had a significant average effect on LBAM (Fig 2A: $F_{1,29}$ = 24.66, P < 0.0001), and on CTM (Fig 2B: $F_{1,30}$ = 4.62, P = 0.040). The larval diet treatment had a significant overall effect on larval development time in both species (LBAM: $F_{2,29}$ = 11.01, P = 0.0004; and CTM: $F_{2,30}$ = 59.95, P < 0.0001). There was also a significant interaction effect between pre-treatment larval parental diet and the treatment larval diet for both species of moth (LBAM: $F_{2,29}$ = 14.50, P < 0.0001; and CTM: $F_{2,30}$ = 19.79, P < 0.0001). In terms of duration of larval development by sex, for LBAM (f: 46.3 $\pm$ 12.6; m: 45.8 $\pm$ 13.6) it did not significantly differ in the experiment ($F_{1,85}$ = 1.89, P = 0.17), however, for CTM (f: 73.3 $\pm$ 24.4; m: 69.0 $\pm$ 22.2) the sexes differed significantly ($F_{1,88}$ = 17.16, P < 0.0001).

Overall, the mean duration of pupal development from pupation to adult eclosion was 9.9 $\pm$ 2.1 days, with a significant difference ($F_{1,63.3}$ = 5.81, P = 0.019) between LBAM (9.5 $\pm$ 2.4 days) and CTM (10.2 $\pm$ 1.7 days). The larval parental pre-treatment diet had a significant average effect on pupal development time for LBAM (Fig 4A: $F_{1,29}$ = 11.26, $\boldsymbol{P}$ < 0.0019), but not for CTM (Fig 4B:

$F_{1,30} = 0.70$, $P = 0.41$). The larval diet treatment did not have a significant overall effect on pupal development time for either species (LBAM: $F_{2,29} = 0.51$, $P = 0.60$; and CTM: $F_{2,30} = 1.57$, $P = 0.23$). There was not a significant interaction effect between pre-treatment larval parental diet and larval diet treatment for either species (LBAM: $F_{2,29} = 1.49$, $P = 0.24$; and CTM: $F_{2,30} = 2.42$, $P = 0.11$). The duration of pupal development by sex for LBAM (f: 9.5 ± 2.3; m: 9.5 ± 2.5) did not significantly differ in the experiment ($F_{1,85} = 0.11$, $P = 0.74$), however for CTM (f: 9.9 ± 1.5; m: 10.5 ± 1.9) the sexes differed significantly ($F_{1,88} = 5.76$, $P = 0.019$) by a small amount.

The mean weight of pupae overall was 27.2 ± 12.0 mg, with a significant amount of overall variation being attributed to the difference ($F_{1,69.2} = 16.21$, $P = 0.0002$) between LBAM (31.6 ± 10.7 mg) and CTM (23.2 ± 11.8 mg). The larval parental pre-treatment diet had a significant average effect on LBAM (Fig 3A: $F_{1,29} = 18.95$, $P = 0.0002$), and for CTM (Fig 3B: $F_{1,30} = 6.66$, $P = 0.015$). The larval diet treatment had a significant overall effect on larval development time in both species (LBAM: $F_{2,29} = 23.82$, $P < 0.0001$; and CTM: $F_{2,30} = 61.89$, $P < 0.0001$). There was also a significant interaction effect between pre-treatment larval parental diet and the larval diet treatment for both species (LBAM: $F_{2,29} = 8.00$, $P = 0.0017$; and CTM: $F_{2,30} = 3.45$, $P = 0.045$). Sex in LBAM (f: 41.2 ± 9.3 mg; m: 25.2 ± 5.5 mg) had a significant effect on pupal weight in the experiment ($F_{1,85} = 224.80$, $P < 0.0001$), with CTM (f: 33.5 ± 10.8 mg; m: 15.6 ± 3.7 mg) exhibiting a similar significant difference ($F_{1,88} = 202.91$, $P < 0.0001$).

The mean weight of adult moths overall was 15.9 ± 10.1 mg, with a significant ($F_{1,69.2} = 4.69$, $P = 0.034$) amount of overall variation being attributed to the difference between LBAM (17.7 ± 9.2 mg) and CTM (14.2 ± 10.6 mg). The larval parental pre-treatment diet had a significant average effect on adult weight in LBAM (Fig 5A: $F_{1,29} = 9.60$, $P = 0.0043$), but not for CTM (Fig 5B: $F_{1,30} = 1.09$, $P = 0.31$). The larval diet treatment had a significant overall effect on adult weight in both species of moth (LBAM: $F_{2,29} = 12.32$, $P = 0.0001$; and CTM: $F_{2,30} = 56.92$, $P < 0.0001$). However, we detected no significant interaction effect between pre-treatment larval parental diet and the larval diet treatment on adult weight for either species (LBAM: $F_{2,29} = 2.80$, $P = 0.077$;

and CTM: $F_{2,30} = 2.14$, $P = 0.13$). Sex in LBAM (f: 26.7 ± 8.1 mg; m: 11.8 ± 3.3 mg) had a significant effect on adult weight in the experiment ($F_{1,85} = 238.37$, $P < 0.0001$), with CTM (f: 24.0 ± 8.5 mg; m: 6.3 ± 2.0 mg) exhibiting a similar significant difference ($F_{1,88} = 320.02$, $P < 0.0001$).

Fecundity, in terms of number of eggs laid per clutch by females arising from the experiment varied widely for both LBAM (21.3 ± 25.5 eggs) and CTM (14.2 ± 10.6 eggs). The larval parental pre-treatment diet did not have a significant average effect on the number of eggs per clutch in female offspring for LBAM (Fig 6A: $F_{1,160} = 0.001$, $P = 0.97$) or for CTM (Fig 6B: $F_{1,418} = 0.80$, $P = 0.37$). The larval diet treatment also did not have a significant overall effect on the number of eggs per clutch in either species (LBAM: $F_{2,160} = 2.88$, $P = 0.059$; and CTM: $F_{2,418} = 2.12$, $P = 0.12$). There was, however, a significant interaction effect between pre-treatment larval parental diet and the larval diet treatment on eggs per clutch for both species (LBAM: $F_{2,160} = 11.48$, $P < 0.0001$; and CTM: $F_{2,418} = 11.81$, $P < 0.0001$).

4 | Discussion

Here we demonstrate a range of effects of parental larval diet and offspring larval diet on several life history traits of two moth species, CTM and *E. postvitanna*. We analysed the effect of parental larval diet (independently of offspring larval diet), and the effect of the offspring larval diet (independently of parental larval diet) on developmental performance (growth and reproduction) of the offspring. A key finding we discuss below is the complex interactions we observed between parental diet (pre-treatment) and larval diet (treatment) in our experiments on various traits important for life history and population growth.

While it was not expressly an objective of this study to compare these two species of moth, as interspecific differences are not unexpected, and were demonstrated in a previous study (Zielonka *et al*., 2021), we show here that transgenerational dietary changes may affect different species differently. We found that survivorship and pupal development time in LBAM were affected by larval parental diet (pre-treatment), but not by larval offspring diet (treatment). It is possible that prolonged development affected by transgenerational dietary changes may influence survival due to the impact that this has on the temporal exposure of offspring to predators and parasitoids (Thiery & Moreau, 2005). Such phenomenon may reflect the slow-growth–high-mortality hypothesis that predicts that prolonged development in herbivorous insects increases mortality as a result of greater exposure to natural enemies (Benrey & Denno, 1997), however, it has been shown that this hypothesis may not always be applicable to all systems (Medina *et al*., 2005; Cornelissen & Stiling, 2006; Chen & Chen, 2018).

Furthermore, we show here that for either species of moth, parental diet, as well as diet of progeny larvae significantly affected the duration of larval development, and the pupal weight of offspring. We also demonstrate that the change from parental diet to offspring diet (the main transgenerational effect) had a significant effect on the same traits either, for LBAM, or CTM. Previous work on transgenerational effects on offspring growth and reproduction have shown that

parental diet (or maternal diet) can affect life history parameters differently, either in Lepidopteran species, (Triggs & Knell, 2012; Kangassalo *et al*., 2020; Rosvik *et al*., 2020), or in other arthropod species (Fox & Mousseau, 1998; Valtonen *et al*., 2012). By contrast, Littlefair & Knell (2016) showed that diet composition has no transgenerational effects on the life history traits of offspring of the Indian meal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (Littlefair & Knell, 2016). Rosvik *et al*., (2020), however, showed that, regardless of the lack of effect of parental diet on duration of larval development of *S. littoralis,* this attribute can be still affected by offspring treatment (Rosvik *et al*., 2020). Interpretations of our results are further complicated by analysing pupal weight between sexes. Our study shows, that transgenerational changes in diet affected either LBAM or CTM female larvae producing, as a result, significantly heavier pupae than male larvae. Acknowledging the fact that shorter duration of the larval development can produce heavier pupae (Barbosa & Capinera, 1977; Rossiter, 1991; Yu *et al*., 2016), it is possible that female larvae in our experiment exhibited shorter duration of larval development than male larvae, which is generally common phenomena in species of Lepidoptera (Danthanarayana, 1975; Miller *et al*., 1982). We demonstrate here, however, that the differences between sexes in duration of larval and pupal development for LBAM are not significant. CTM female larvae, however, exhibited significantly longer duration of larval development than male larvae, but shorter pupal development analogous to significantly longer in males. However, we found no overall differences in larval survivorship, which corroborates with other similar studies, e.g. for the rice bloodworm, *Chironomus tepperi* Skuse (Diptera: Chironomidae) (Colombo *et al*., 2014), or for *S. littoralis* (Rosvik *et al*., 2020).

It is possible that the effect of parental diet on performance observed in our study may reflect different utilisation abilities (Roslin & Salminen, 2008) or development strategies of the larvae when exposed to a change diet quality (Damman, 1987; Abarca *et al*., 2014). There is evidence that food quality or dietary restrictions in the parental diet can affect life history traits of offspring transgenerationally, and when both parents are fed on a poor diet, offspring tends to invest in body

size, but not in immunity (Triggs & Knell, 2012). It would appear that transgenerational response in our study may be largely governed by either the quality of a diet, or genetic predisposition to food. It is possible that transgenerational effects may be linked to nutrition causing epigenetic changes through DNA methylation and gene expression (Colombo *et al*., 2014), and as a result, may show substantial transgenerational phenotypic plasticity affecting morphological and physiological traits in insects (Colombo *et al*., 2014; Rösvik *et al*., 2020).

Interestingly, parental diet and the offspring diet did not affect fecundity (egg clutch size) of the offspring in our study. Transgenerational effect of parental diet, however, had a significant effect on the oviposition of progeny female adult. The change in diet resulted in significant differences in the size of egg clutches produced by females of both species of moth. Perhaps transgenerational changes in host plant experienced by a larva may influence the phenotypic plasticity of the adult female ovipositional behaviour of these two polyphagous species (Gu & Danthanarayana, 2000; Thöming *et al*., 2013). Such a response may be a form of a spatial distribution or exploration strategy to a new unknown habitat, or as a response to new patterns within the habitat in terms of egg survival strategy and their protection against predators (Görür, 2005; Fusco & Minelli, 2010). It is unclear, however, how dietary changes experienced by a limited range of genotypes in this study can affect a complex phenotypic plasticity across various traits of these two moth species (Wootton, 1994; Fox & Mousseau, 1998; Rösvik *et al*., 2020). Despite there being several approaches to investigate the complex indirect interactions that occur within multi-species communities, explaining individual mechanisms remains challenging (Wootton, 1994; Wajnberg *et al*., 2001; Shennan, 2008).

It is possible that the information about the physiochemical characteristics of the host plant on which larvae were developing remained through the metamorphosis and was reflected by the ovipositional behaviour of the female adults (Anderson *et al*., 2013; Petit *et al*., 2015; Proffit *et al*., 2015). We hypothesise that leaf size or shape, resource abundance or olfactory cues may be amongst other complex factors that influence life history variation in traits such as clutch size, as

has been shown for other lepidopterans (Kagata & Ohgushi, 2002; Stefanescu *et al*., 2006; Rizvi & Raman, 2015; Dell'Aglio *et al*., 2016). However, it is possible that females may exhibit different trade-offs in response to a new food resource, for example, by producing smaller size clutches on one known host plant, with the opposite response to an unfamiliar host. For example, in some lepidopterans larger egg clutches tend to be less parasitized than smaller egg clutches (Beckage & Riddiford, 1983; Geervliet *et al*., 1998; Stuart & Polavarapu, 2000; Randlkofer *et al*., 2007). Despite the theory that clutch size is determined by the availability of resources (Godfray *et al*., 1991), perhaps production of larger egg clutches reflects one of the selective pressures necessary for neonates to survive, for example, by building an effective shelter in response to natural enemies along with initial food availability (Damman, 1987).

Our results illustrate that the parental host plant can influence life history variation in progeny transgenerationally in complex ways. This suggests a role for changes in, for example, management of plant diversity in crop habitats as a strategy for pest control where planned, sequential changes in host plant species could be designed to target multiple generations of the same insect pest. It would be difficult, however, to unequivocally interpret and define what sequential changes may be required for improved pest control at this stage, as this may depend on the crop plant species grown, crop species diversity, and perhaps cultural practices, e.g. crop rotation strategies, or crop density. The mechanisms underlying physiological changes in insect performance through transgenerational dietary changes are, however, still unclear.

References

Abarca, M., Boege, K., Zaldívar-Riverón, A. & Giray, T. (2014). Shelter-building behavior and natural history of two pyralid caterpillars feeding on *Piper stipulaceum*. *Journal of Insect Science, 14*, 1–16.

Anderson, P., Sadek, M.M., Larsson, M., Hansson, B.S. & Thöming, G. (2013). Larval host plant experience modulates both mate finding and oviposition choice in a moth. *Animal Behaviour, 85*, 1169–1175.

Barbosa, P & Capinera, J.L. (1977). The influence of food on developmental characteristics of the gypsy moth, *Lymantria dispar* (L.). *Canadian Journal of Zoology, 55*, 1424–1429.

Beckage, N.E. & Riddiford, L.M. (1983). Growth and development of the endoparasitic wasp *Apanteles congregatus*: dependence on host nutritional status and parasite load. *Physiological Entomology, 8*, 231–241.

Beitia, F., Asis, J.D., De Pedro, L., Goula, M. & Tormos, J. (2016). Importance of feeding behaviour on life cycle in the zoophytophagous bug *Dicyphus geniculatus*. *Bulletin of Insectology, 69*, 173–180.

Bell, A.M., & Hellmann, J.K. (2019). An integrative framework for understanding the mechanisms and multigenerational consequences of transgenerational plasticity. *Annual Review of Ecology, Evolution, and Systematics, 50*, 97–118.

Benrey, B. & Denno, R.F. (1997). The slow-growth–high-mortality hypothesis: a test using the cabbage butterfly. *Ecology, 78*, 987–999.

Brewer, J.W., Capinera, J.L., Deshon, R.E. & Walmsley, M.L. (1985). Influence of foliar nitrogen levels on survival, development, and reproduction of western spruce budworm, *Choristoneura occidentals* (Lepidoptera: Tortricidae). *The Canadian Entomologist, 117*, 23–32.

Brockerhoff, E.G. Suckling, D.M., Ecroyd, C.E., Wagstaff, S.J., Raabe, M.C., Dowell, R.V. & Wearing, C.H. (2011). Worldwide host plants of the highly polyphagous, invasive *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Journal of Economic Entomology, 104*, 1514–1524.

Brown, J.W., Epstein, M.E., Gilligan, T.M., Passoa, S.C. & Powell, J.A. (2010). Biology, identification, and history of the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae: Archipini) in California: an example of the importance of local faunal surveys to document the establishment of exotic insects. *American Entomologist, 56*, 34–43.

CABI (2020). *Cacoecimorpha pronubana* and *Epiphyas Postvittana*. In *Invasive Species Compendium*. Wallingford, UK: CAB International. https://www.cabi.org/isc

Chen, K.W., & Chen, Y. (2018). Slow-growth high-mortality: A meta-analysis for insects. *Insect science*, *25*, 337–351.

Colombo, V., Pettigrove, V.J., Golding, L.A. & Hoffmann, A.A. (2014). Transgenerational effects of parental nutritional status on offspring development time, survival, fecundity, and sensitivity to zinc in *Chironomus tepperi* midges. *Ecotoxicology and Environmental Safety, 110*, 1–7.

Copping, L.G. & Menn, J.J. (2000). Biopesticides: a review of their action, applications and efficacy. *Pest Management Science: Formerly Pesticide Science*, *56*, 651–676.

Cornelissen, T., & Stiling, P. (2006). Does low nutritional quality act as a plant defence? An experimental test of the slow-growth, high-mortality hypothesis. *Ecological Entomology, 31*, 32–40.

Damalas, C.A., & Koutroubas, S.D. (2016). Farmers' exposure to pesticides: toxicity types and ways of prevention. *Toxics, 4*, 1.

Damman, H. (1987). Leaf quality and enemy avoidance by the larvae of a pyralid moth. *Ecology, 68*, 88–97.

Danthanarayana, W. (1975). The bionomics, distribution and host range of the light brown apple moth, *Epiphyas postvittana* (Walk.) (Tortricidae). *Australian Journal of Zoology, 23*, 419–437.

Dell'Aglio, D.D., Losada, M.E., & Jiggins, C.D. (2016). Butterfly learning and the diversification of plant leaf shape. *Frontiers in Ecology and Evolution, 4*, 81.

Dhawan, A., & Peshin, R. (2009). Integrated pest management: concept, opportunities and challenges. In *Integrated pest management: innovation-development process*, pp. 51–81. Dordrecht: Springer.

EPPO. (2020). *PQR database*. Paris, France: European and Mediterranean Plant Protection Organization.

Feng, Y., Wratten, S., Sandhu, H., & Keller, M. (2015a). Interspecific competition between two generalist parasitoids that attack the leafroller *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Bulletin of Entomological Research, 105*, 426–433.

Feng, Y., Wratten, S., Sandhu, H., & Keller, M. (2015b). Host plants affect the foraging success of two parasitoids that attack light brown apple moth *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae). *PloS One, 10*, 4.

Fisher, R.C. (1924). The life-history and habits of *Tortrix pronubana*, Hb., with special reference to the larvae and pupal stages. *Annals of Applied Biology, 11*, 395–447.

Fox, C.W. & Mousseau, T.A. (1998). Maternal effects as adaptations for transgenerational phenotypic plasticity in insects. In *Maternal effects as adaptations*, pp. 159–177. Oxford, UK: Oxford University Press.

Freitak, D., Heckel, D.G., & Vogel, H. (2009). Dietary-dependent trans-generational immune priming in an insect herbivore. *Proceedings of the Royal Society B: Biological Sciences, 276*, 2617–2624.

Fusco, G. & Minelli, A. (2010). Phenotypic plasticity in development and evolution: facts and concepts. *The Royal Society, 356*, 547–556.

Gaines, T.B. (1969). Acute toxicity of pesticides. *Toxicology and Applied Pharmacology, 14*, 515–534.

Geervliet, J.B., Vreugdenhil, A.I., Dicke, M. & Vet, L.E. (1998). Learning to discriminate between infochemicals from different plant-host complexes by the parasitoids *Cotesia glomerata* and *C. rubecula. Entomologia Experimentalis et Applicata, 86*, 241–252.

Godfray, H.C.J., Partridge, L. & Harve, P.H. (1991). Clutch size. *Annual Review of Ecology and Systematics, 22*, 409–429.

Görür, G. (2005). *The importance of phenotypic plasticity in herbivorous insect speciation. Insect Phenotypic Plasticity. Diversity of Responses*, pp. 145–172. Science Publishers Inc.

Gu, H. & Danthanarayana, W. (2000). Variations in life history traits and flight capacity among populations of the light brown apple moth *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae). *Australian Ecology, 25*, 571–579.

Harmon, E.A. & Pfennig, D.W. (2021). Evolutionary rescue via transgenerational plasticity: Evidence and implications for conservation. *Evolution & Development, 23*, 292–307.

Kaçar, G. & Ulusoy, M.R. (2008). A new pest of olive trees: Carnation tortrix, *Cacoecimorpha pronubana* (Hübner), 1796–1799 (Lepidoptera: Tortricidae) in the Eastern Mediterranean Region of Turkey. *Türkiye Entomoloji Dergisi, 32*, 211–223.

Kaçar, G. & Ulusoy, M.R. (2012). Karanfil yaprakbükeni, *Cacoecimorpha pronubana* (Hübner) (Lepidoptera: Tortricidae)'nın zeytin bahçelerindeki parazitoit ve predatörleri. *Türkiye Biyolojik Mücadele Dergisi, 3*, 13–20.

Kagata, H. & Ohgushi, T. (2002). Oviposition stimuli for host plant recognition and clutch size determination in a leaf-mining moth. *Ecological Entomology, 27*, 622–625.

Kangassalo, K., Sorvari, J., Nousiainen, I., Pölkki, M., Valtonen, T.M., Krams, I. & Rantala, M.J. (2020). Intra-and trans-generational phenotypic responses of the greater wax moth, *Galleria mellonella*, to a low-nutrition larval diet. *Annales Zoologici Fennici, 57*, 99–114.

Knight, A.L. (2014). Multiple mating of male and female codling moth (Lepidoptera: Tortricidae) in apple orchards treated with sex pheromone. *Environmental Entomology, 36*, 157–164.

Kobiela, M.E., & Snell-Rood, E.C. (2018). Nickel exposure has complex transgenerational effects in a butterfly. *Integrative and comparative biology, 58*, 1008–1017.

Lance, D.R. (2012). *Host-seeking behavior of the gypsy moth: the influence of polyphagy and highly apparent host plants. Herbivorous Insects: Host-Seeking Behavior and Mechanisms*. New York: Academic Press. 201 pp.

Littlefair, J.E. & Knell, R.J. (2016). Within-and trans-generational effects of variation in dietary macronutrient content on life-history traits in the moth *Plodia interpunctella*. *Plos One, 11*, 1–16.

Lo, P.L., Suckling, D.M., Bradley, S.J., Walker, J.T.S., Shaw, P.W. & Burnip, G.M. (2000). Factors affecting feeding site preferences of lightbrown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae), on apple trees in New Zealand. *New Zealand Journal of Crop and Horticultural Science, 28*, 235–243.

Matos, E.L., Loria, D.I., Albiano, N., Sobel, N., & de Buján, E.C. (1987). Pesticides in intensive cultivation: effects on working conditions and workers' health. *Bulletin of the Pan American Health Organization, 21*, 405–416.

Medina, R.F., Barbosa, P., & Waddell, K. (2005). Parasitism levels in *Orgyia leucostigma* feeding on two tree species: implications for the slow-growth-high-mortality hypothesis. *Entomologia Experimentalis et Applicata, 115*, 193–197.

Miller, T.A., Highfill, J.W., & Cooper, W.J. (1982). Relationships between pupal size and sex in giant silkworm moths (Saturniidae). *Journal of the Lepidopterists' Society, 36*, 207–216.

Moreau, J., Desouhant, E., Louâpre, P., Goubault, M., Rajon, E., Jarrige, A., Menu, F., & Thiéry, D. (2017). How host plant and fluctuating environments affect insect reproductive strategies? *Advances in Botanical Research, 81*, 259–287.

Pencheva, A., & Yovkova, M. (2016). New data on alien insect pests of ornamental plants in Bulgaria. *Forestry Ideas, 22*, 17–33.

Petit, C., Le Ru, B., Dupa, S., Frérot, B., Ahuya, P., Kaiser-Arnauld, L., Harry, M., & Calatayud, P.A. (2015). Influence of dietary experience on the induction of preference of adult moths and larvae for a new olfactory cue. *Plos One, 10*, 8.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2020). nlme: Linear and Nonlinear Mixed Effects Models. *R package version 3.1–149*, <URL: https://CRAN.R-project.org/package=nlme>.

Proffit, M., Khallaf, M.A., Carrasco, D., Larsson, M.C., & Anderson, P. (2015). 'Do you remember the first time?'. Host plant preference in a moth is modulated by experiences during larval feeding and adult mating. *Ecology Letters, 18*, 365–374.

R Core Team. (2020). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Randlkofer, B., Obermaier, E., & Meiners, T. (2007). Mother's choice of the oviposition site: balancing risk of egg parasitism and need of food supply for the progeny with an infochemical shelter? *Chemoecology, 17*, 177–186.

Rizvi, S.Z., & Raman, A. (2015). Oviposition behaviour and life-history performance of *Epiphyas postvittana* (Lepidoptera: Tortricidae) on the leaves of *Vitis vinifera* (Vitales: Vitaceae) infected with *Botrytis cinerea* (Helotiales: Sclerotiniaceae). *VITIS-Journal of Grapevine Research, 54,* 151–159.

Reddy, P.P. (2016). Insects Pests and Their Management. In *Sustainable Crop Protection under Protected Cultivation*, pp.187–206. Netherlands: Springer.

Roslin, T., & Salminen, J.P. (2008). Specialization pays off: contrasting effects of two types of tannins on oak specialist and generalist moth species. *Oikos, 117*, 1560–1568.

Rossiter, M.C. (1991). Maternal effects generate variation in life history: consequences of egg weight plasticity in the gypsy moth. *Functional Ecology, 5*, 386–393.

Rösvik, A., Lhomme, P., Khallaf, M.A., & Anderson, P. (2020). Plant-induced transgenerational plasticity affecting performance but not preference in a polyphagous moth. *Frontiers in Ecology and Evolution, 8*, 254.

Shennan, C. (2008). Biotic interactions, ecological knowledge and agriculture. *Philosophical Transactions of the Royal Society B: Biological Sciences, 363*, 717–739.

Solomon, M.G., Jay, C.N., Innocenzi, P.J., Fitzgerald, J.D., Crook, D., Crook, A.M., Easterbrook, M.A., & Cross, J.V. (2001). Natural enemies and biocontrol of pests of strawberry in northern and central Europe. *Biocontrol Science and Technology, 11*, 165–216.

Stefanescu, C., Peñuelas, J., Sardans, J., & Filella, I. (2006). Females of the specialist butterfly *Euphydryas aurinia* (Lepidoptera: Nymphalinae: Melitaeini) select the greenest leaves of *Lonicera implexa* (Caprifoliaceae) for oviposition. *European Journal of Entomology, 103*, 569.

Stenersen, J. (2004). *Chemical pesticides mode of action and toxicology*. Boca Raton, FL, USA: CRC Press.

Stuart, R.J., & Polavarapu, S. (2000). Egg-mass variability and differential parasitism of *Choristoneura parallela* (Lepidoptera: Tortricidae) by endemic *Trichogramma minutum* (Hymenoptera: Trichogrammatidae). *Annals of the Entomological Society of America, 93*, 1076–1084.

Suckling, D.M., & Brockerhoff, E.G. (2010). Invasion biology, ecology, and management of the light brown apple moth (Tortricidae). *Annual Review of Entomology, 55*, 285–306.

Thiery, D., & Moreau, J. (2005). Relative performance of European grapevine moth (*Lobesia botrana*) on grapes and other hosts. *Oecologia, 143*, 548.

Thöming, G., Larsson, M.C., Hansson, B.S., & Anderson, P. (2013). Comparison of plant preference hierarchies of male and female moths and the impact of larval rearing hosts. *Ecology, 94*, 1744–1752.

Triggs, A.M., & Knell, R.J. (2012). Parental diet has strong transgenerational effects on offspring immunity. *Functional Ecology, 26*, 1409–1417.

Wajnberg, E., Scott, J.K., & Quimby, P.C. Eds. (2001). *Evaluating indirect ecological effects of biological control*. Wallingford, UK: CABI.

Wang, Y., Wu, C., Cang, T., Yang, L., Yu, W., Zhao, X., Wang, Q., & Cai, L. (2014). Toxicity risk of insecticides to the insect egg parasitoid *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae). *Pest Management Science, 70*, 398–404.

Wootton, J.T. (1994). The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics, 25*, 443–466.

Valtonen, T.M., Kangassalo, K., Pölkki, M., & Rantala, M.J. (2012). Transgenerational effects of parental larval diet on offspring development time, adult body size and pathogen resistance in *Drosophila melanogaster*. *Plos One, 7*, 1–9.

Van Lenteren, J.C. (2000). A greenhouse without pesticides: fact or fantasy? *Crop Protection, 19*, 375–384.

Yazdani, M., Feng, Y., Glatz, R., & Keller, M.A. (2015). Host stage preference of *Dolichogenidea tasmanica* (Cameron, 1912) (Hymenoptera: Braconidae), a parasitoid of *Epiphyas postvittana* (Walker, 1863) (Lepidoptera: Tortricidae). *Austral Entomology, 54*, 325–331.

Yu, Q., Wang, F., Zhang, R., Guo, G., Fan, R., & Hao, C. (2016). Effects of pupal weight on the fecundity and longevity of adults and the larval development of the next generation in *Grapholitha molesta* (Lepidoptera: Tortricidae). *Acta Entomologica Sinica, 59*, 985–990.

Zielonka, M.W., Harris, W.E., Pope, T.W., & Leather, S.R. (2021). Abundance and phenology of two pest species, *Cacoecimorpha pronubana* and *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Annals of Applied Biology, 179*, 207–215.

Figure captions

Figure 1. The number of surviving larvae (from five) were counted across two factors, the pre-treatment parental diet and the treatment larval diet. The bar shading reflects the respective larval diet treatment labelled on the x axis. Dots indicate individual larval count per plant across the experimental treatments. Panel A show data for LBAM and panel B shows data for CTM.

Figure 2. Individual larval development time (in days) were counted across two factors, the pre-treatment parental diet and the treatment larval diet. The bar shading reflects the respective larval diet treatment labelled on the x axis. Dots indicate individual larvae measured across the experimental treatments. Panel A show data for LBAM and panel B shows data for CTM.

Figure 3. Individual pupal weight (milligrams) were counted across two factors, the pre-treatment parental diet and the treatment larval diet. The bar shading reflects the respective larval diet treatment labelled on the x axis. Dots indicate individual larvae measured across the experimental treatments. Panel A show data for LBAM and panel B shows data for CTM.

Figure 4. Individual pupal development time (in days) were counted across two factors, the pre-treatment parental diet and the treatment larval diet. The bar shading reflects the respective larval diet treatment labelled on the x axis. Dots indicate individual larvae measured across the experimental treatments. Panel A show data for LBAM and panel B shows data for CTM.

Figure 5. Individual adult weight (in milligrams) were counted across two factors, the pre-treatment parental diet and the treatment larval diet. The bar shading reflects the respective larval diet treatment labelled on the x axis. Dots indicate individual larvae measured across the experimental treatments. Panel A show data for LBAM and panel B shows data for CTM.

Figure 6. Individual count of eggs per clutch across two factors, the pre-treatment parental diet and the treatment larval diet. The bar shading reflects the respective larval diet treatment labelled on the x axis. Dots indicate individual larvae measured across the experimental treatments. Panel A show data for LBAM and panel B shows data for CTM.

A

(LBAM) Pre-Treatment

B

(CTM) Pre-Treatment

A

(LBAM) Pre-Treatment

B

(CTM) Pre-Treatment

A

(LBAM) Pre-Treatment

B

(CTM) Pre-Treatment