

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Developmental stage-dependent response and preference for host plant quality in an insect herbivore

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ARTICLE INFO

Article history:

Received 10 July 2018

Initial acceptance 27 August 2018

Final acceptance 21 December 2018

MS. number: 18-00479R

Keywords:

butterfly

developmental stress

drought stress

food choice

oviposition choice

preference–performance hypothesis

Larval-derived nutritional reserves are essential in shaping insects' adult fitness. Early larval instars of many Lepidopteran species are often sessile, and the conditions experienced by these larvae are often highly dependent on the mother's oviposition choice. Later larval stages are more mobile and therefore can choose their food whenever alternatives are available. We tested how feeding on a drought-exposed host plant impacts life history in an insect herbivore, and whether the observed responses depended on developmental stage. We used drought to alter host plant quality of the ribwort plantain, *Plantago lanceolata*, and assessed whether host plant preference of postdiapause larvae and adult females increased their own or their offspring's performance, respectively, in the Glanville fritillary butterfly, *Melitaea cinxia*. Larval response to drought-exposed host plants varied with developmental stage: early larval stages (prediapause) had decreased survival and body mass on drought-exposed plants, while later larval stages (postdiapause) developed faster, weighed more and had a higher growth rate on the drought-exposed plants. Postdiapause larvae also showed a preference for drought-exposed host plants, i.e. those that increased their performance, but only when fed on well-watered host plants. Adult females, on the other hand, showed an oviposition preference for well-watered plants, hence matching the performance of their prediapause but not their postdiapause offspring. Our results highlight how variation in environmental conditions generates stage-specific responses in insects. Individuals fine-tune their own or their offspring's diet by behavioural adjustments when variation in host plant quality is available.

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Nutrition has an essential role in the development and maturation of individuals, and the conditions experienced and resources acquired during development translate to resource allocation among key life history traits throughout an individual's life (Clissold & Simpson, 2015; Nestel et al., 2016). This is also the case in many insects, where a sufficient amount of nutrients needs to be acquired during development, and then utilized during larval, pupal and adult stages (Nestel et al., 2016). The energetic demands and nutritional requirements may, however, differ depending on the organism's life stage. Amino acids, for example, are utilized at larval stages for growth and development, whereas in adults proteins are allocated to reproduction (i.e. egg/sperm production) and body maintenance (i.e. life span; Barrett, Hunt, Moore, & Moore, 2009; Rodrigues et al., 2015; Simpson, Raubenheimer, Behmer,

Whitworth, & Wright, 2002). For herbivorous insects, the primary and secondary metabolites, as well as specific nutrients such as nitrogen, are acquired from the host plants the individuals feed on (Machovsky-Capuska, Senior, Simpson, & Raubenheimer, 2016; Nestel et al., 2016). Alterations in the essential metabolites and in interactions among nutrients (i.e. nutritional balance) have been shown to impact life history traits across life stages, for example reproductive performance, life span and immunology (e.g. Cotter, Simpson, Raubenheimer, & Wilson, 2011; Jensen, McClure, Priest, & Hunt, 2015; Lee et al., 2008; Maklakov et al., 2008; Runagall-McNaull, Bonduriansky, & Crean, 2015; Simpson et al., 2015). The nutritional value (i.e. quality) of the host plant can, however, also vary greatly within species, owing to differences in genetic background, plant ontogeny, biotic stressors and environmental conditions experienced by the host plant (Atkinson & Urwin, 2012; Awmack & Leather, 2002; Rodrigues et al., 2015).

In Lepidoptera, the larvae, especially during the early stages, are often sessile, and hence the mother's choice of a host plant determines the conditions the offspring experience, consequently impacting their development and survival (Jaumann & Snell-Rood,

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2017; Rausher, 1979). Accordingly, the preference–performance hypothesis predicts that females should prefer to lay eggs on host plant species that increase their offspring's performance and fitness. Most studies on the preference–performance hypothesis have focused on the female's choice of host plant species (Gripenberg, Mayhew, Parnell, & Roslin, 2010). The few studies that have assessed female preference for individuals within a host plant species often show positive correlation with the offspring's performance (Heisswolf, Obermaier, & Poethke, 2005; Wise & Weinberg, 2002). Examples of a mismatch between the mother's preference and offspring's performance also exist, but mainly in relation to between-species preference–performance associations (e.g. Gamberale-Stille, Söderlind, Janz, & Nylin, 2014; Karolewski et al., 2017). In cases where the host plant requirements differ between the developmental stages of the larvae, conflicts may arise. However, the later developmental stages are likely to be less dependent on the maternal choice of the host plant, as individuals at this stage are often more mobile and can potentially choose a diet that best matches their own performance. Generally, the evolution between the female's oviposition preference and offspring's performance is impacted by host plant variation within a landscape as well as changing environmental conditions, all of which modify plant–insect interactions (Thompson, 1988).

An environmental condition likely to impact both host plants and herbivores feeding on them is drought. As drought, in general, has been predicted to increase in frequency in the future (Bale et al., 2002; Morecroft, Bealey, Howells, Rennie, & Woiwod, 2002), understanding how it will impact the life history of individuals and potentially the performance of populations, communities and ecosystems is of crucial importance. Drought stress responses in plants are complex, and include accumulation of carbohydrates, soluble proteins and free amino acids, together with alterations in the levels of secondary metabolites (Chaves, Maroco, & Pereira, 2003; Farooq, Wahid, Kobayashi, Fujita, & Basra, 2009). These responses also depend on the magnitude and the duration of the stress. Under mild and high levels of drought stress, photosynthesis has generally been shown to decline, with the concentration of nitrogen and sugars increasing and concentration of secondary metabolites decreasing in the plant tissue (Gutbrodt, Mody, & Dorn, 2011; Huberty & Denno, 2004; Mattson & Haack, 1987). Plants also control water status immediately by closing the stomata and by inhibiting leaf growth to protect them from prolonged water loss (Chaves et al., 2003). All these changes in the host plant in response to exposure to water limitation are likely to have consequences also for the performance of organisms utilizing them, with potential impact on their foraging behaviour and decisions (Lenhart, Eubanks, & Behmer, 2015; Veteli, Kuokkanen, Julkunen-Tiitto, Roininen, & Tahvanainen, 2002). Yet studies on the effects of host plant drought on plant–herbivore interactions are still limited (but see Bauerfeind & Fischer, 2013; Jamieson, Trowbridge, Raffa, & Lindroth, 2012; Lenhart et al., 2015).

Here, we used the Glanville fritillary butterfly, *Melitaea cinxia*, and one of its host plant species, *Plantago lanceolata*, to assess the effects of drought-exposed host plants on life history variation and behaviour on this insect herbivore. In Finland, the butterfly exists at its northern range limit and is found in dry meadows on rocky outcrops and pastures (Ojanen, Nieminen, Meyke, Pöyry, & Hanski, 2013). In these habitats, females tend to prefer warm microclimatic conditions for oviposition, exposing their offspring to the risk of feeding on host plants that may at times experience even severe drought (M. Saastamoinen, personal observation). Reduced precipitation over summer is also known to be the major driver of decreased population growth at the metapopulation level (Kahilainen, van Nouhuys, Schulz, & Saastamoinen, 2018). We were specifically interested in (1) the responses of the larvae feeding on

host plants that had been exposed to relatively long-lasting drought stress accounting for the potential differences in response between the developmental stage of the larvae (pre-versus postdiapause), (2) whether the developmental responses translate to carryover effects on adult fitness-related traits, and (3) whether postdiapause larvae or adult females show a preference for a host plant type that correlates with their own or their offspring performance, respectively.

METHODS

Study System

In Finland, the Glanville fritillary is present only in the Åland Islands archipelago, southwest Finland, where it persists as a classic metapopulation, with a high turnover of local populations (Hanski, 1999). The ca. 4000 suitable habitat patches for the butterfly in Åland are defined by the presence of at least one of the host plant species, *P. lanceolata* or *Veronica spicata* (Ojanen et al., 2013). Changes in population dynamics and size are greatly influenced by environmental conditions, such as temperature and precipitation, which are partially driven by their impact on host plant quality, for example desiccation during drought periods (Kahilainen et al., 2018; Tack, Mononen, & Hanski, 2015). During early summer females eclose and mate, after which they locate suitable host plants in which to oviposit. Females lay several clutches of 100–200 eggs each (Saastamoinen, 2007). The first-instar larvae are sessile and feed gregariously mostly on the host plant on which their mother oviposited them. At the beginning of autumn, the larvae spin a silk web in which they overwinter as a group. Larger families and those with heavier larvae have higher overwinter survival (Kuussaari & Singer, 2017; Saastamoinen, Hirai, & van Nouhuys, 2013). In spring, the larvae initiate feeding on newly grown host plants. At this stage, the larvae grow the most (Saastamoinen et al., 2013), become solitary and can move over longer distances (i.e. tens of metres) in search of food (Kuussaari, van Nouhuys, Hellmann, & Singer, 2004).

Ethical Note

The species used in the assays is not considered endangered and is not protected; thus, no federal permits were required to perform research on these insects. The individuals derived from a laboratory stock and all procedures used delicate and round-end tweezers that minimized any stress on the individuals during the experimental manipulation. We ensured that they were kept in large containers and cages to avoid additional stress due to growing. We adhered to the ASAB/ABS guidelines for the treatment of animals.

Plant Material Used for the Experiments

All plants were grown from field-collected seeds originating from eight different local populations across the main island of Åland. Once the plants reached 10 cm shoot length, they were potted singly using fertilized soil 15%:25%:25%, peat:perlite:sand, with a neutral pH. Plants were reared individually in well-watered 0.7-litre pots in designed blocks in common garden conditions (26:18 °C; 15:9 h light:dark). Each block contained both types of host plants and their location in the greenhouse was randomized throughout the experiment. Once the plants were full size we initiated the treatments: the well-watered, turgid, plants received 50 ml of water every third day, whereas the drought-exposed host plants received only 20 ml of water every third day. As *P. lanceolata* in the Åland islands occurs on open pastures and dry meadows we ensured that in the well-watered treatment the soil dried out fully

before the next watering event took place (based on a pilot experiment, data not shown). However, to ensure significant changes in the plants, the drought treatments were started 12 weeks before the feeding treatments were initiated. At this point the plants presented some phenotypical differences between treatments: well-watered plants seemed to have more, thinner and lighter green leaves than the drought-exposed plants (A.L. Salgado, personal observation). A total of 193 well-watered and 218 drought-exposed plants were used in the experiments. For all experiments described below, the larvae were provided with either 'well-watered' or 'drought-exposed' *P. lanceolata* leaves, randomly picked from each treatment group on a daily basis.

Larval Rearing and Experimental Set-Ups

For logistic reasons (i.e. seed collection can only be done in late autumn) the experiment was initiated after the larval diapause was broken. Hence the traits were measured at the postdiapause, pupal, adult and prediapause stages (second generation), over the life cycle of the individuals.

Postdiapause Larval Rearing and Food Plant Choice Test

For the experiment, we reared in total 185 larvae from 13 laboratory-generated families. For logistic reasons, the larvae from each family were woken up from diapause in three different sets (12, 19 and 26 April 2017). The larvae were reared in family groups in mesh-covered containers with filter paper and fed ad libitum with leaves of well-watered host plants until they reached the final, seventh instar (28:15 °C; 12:12 h light:dark). Owing to their dark colour and preference for warm microclimatic conditions in the field, the larvae often experience temperatures much higher than the ambient conditions (up to 35 °C; Kallioniemi & Hanski, 2011). The humidity conditions within the room ranged between 40 and 60% (day:night). However, to ensure higher relative humidity (80%) within the containers we sprayed additional water on the filter paper. At the beginning of the seventh instar, individuals were randomly assigned to feed on either well-watered ($N = 92$) or drought-exposed ($N = 93$) host plants (see above), ensuring that individuals from different families were spread across treatments. From this stage onwards, larvae were kept individually in 100 ml transparent containers; they received the assigned diet and were otherwise reared as described above.

For the postdiapause food plant choice trials, we marked six equally spaced numbers on paper discs placed on 150 mm petri dishes. On each number, we placed a leaf piece 1.2 cm in diameter, from either the well-watered or drought-exposed treatment, using a drop of water to stick and flatten the discs. The type of leaf used (well-watered versus drought-exposed) was randomly alternated between odd and even numbers in each trial. The leaves used in the assay were collected from the plants in the morning before each trial. We used a cork borer to punch the leaves, and kept the leaf discs fresh by maintaining them inside a cold box with ice packs before each trial. For each trial, a single larva was set in the middle of the petri dish. Thirty minutes later, the test was terminated, the larva was placed back in its container and feeding was continued ad libitum with the assigned host plant. After each food choice test, the leaf discs were pasted onto white paper and scanned for further analysis of the area consumed. We used Fiji 2.0 software (Schindelin et al., 2012) to measure the leaf area left of every disc. To obtain the area eaten of each leaf disc, we subtracted the area left from the initial area (1.13 cm²). For each individual tested, the food plant choice trials were carried out three times, on days 2, 3 and 4 of the seventh instar. Prior to the test, each larva was deprived of food the night before. All trials were run between 1000 and 1300 hours

at 28 °C. Finally, all individuals were weighed at pupation (resolution of 0.01 mg on an XS105 analytical balance, Mettler Toledo, Greifensee, Switzerland).

Host Plant Choice and Larval Rearing

Once pupae eclosed, individuals were sexed and placed in cylindrical cages (29 × 13 cm³) with no more than 25 individuals per cage. Matings took place when the individuals were on average 2 days old (range 1–7 days). To ensure a successful number of matings, each mating cage contained a 2:1 male-biased sex ratio. All males used for the mating were from the well-watered host plant treatment. They were obtained by rearing an extra set of larvae ($N = 101$) with well-watered host plant leaves; they came from the same families as above and were otherwise identically treated. Inbreeding was avoided by ensuring that individuals from the same family were not placed in the same mating cage. Matings occurred between 0900 and 1600 hours at a constant temperature of 26 °C. After mating, females were placed into oviposition cages (60 × 60 cm and 50 cm high) covered with nylon net; males were killed. All individuals were provided with fresh 20% honey:80% water every day and dead individuals were recorded.

We used a total of 66 mated females for testing oviposition host plant choice. For each trial, two well-watered and two drought-exposed host plants were placed within the oviposition cages, 20 cm apart (the host plant location was alternated in each trial). The plants were chosen to appear similar phenotypically, with a comparable amount of leaves and height. Each female was kept in the oviposition cage for 24 h, after which the host plants were inspected for egg clutches. As females rarely lay eggs on 2 consecutive days, and as the number of oviposition cages was limited, we removed the females from the oviposition cage once they had laid eggs and placed them together with other mated females for 24 h before their next oviposition trial. The oviposition choice of each female was assessed three times after which they were placed into a 2-litre netted cage with a well-watered host plant to assess female lifetime egg production and life span.

The egg clutches from each female were maintained under common garden conditions (28:15 °C; 12:12 h light:dark; 80% relative humidity) on petri dishes (100 mm). For each clutch, we counted eggs at day 4 after oviposition and larvae in each clutch once they hatched. To assess the performance of prediapause larvae on the two types of diet, we used the eggs from the first clutch of each female ($N = 49$). Forty larvae per clutch were split between the host plant diets (i.e. 20 larvae in each treatment group): well-watered and drought-exposed. The larvae were kept in petri dishes containing a filter paper, and new leaves from the treatment plants were added ad libitum each day. As before, water was sprayed each day on the filter paper to ensure higher humidity and old leaves were removed only after all larvae had moved to a fresh leaf. The prediapause larvae spin a silken web throughout development, which helps them to maintain optimal microclimate conditions, and we carefully avoided destroying these webs during the experiment. We measured the prediapause development time, weight and survival at diapause.

Statistical Analyses

The statistical analyses were performed in R software (R Core Team, 2015) using lme4, lmerTest, MASS and glmmTMB packages with the corresponding lmer, glmer and glmmTMB functions to fit the models (Bates, Mächler, Bolker, & Walker, 2015; Brooks et al., 2017; Kuznetsova, Brockhoff, & Christensen, 2017; Venables & Ripley, 2002). We constructed a full model for each response variable with second-order interactions included. The models were validated by

checking overdispersion (when needed), plotting the residuals against the fitted values, and verified for normality by plotting the residuals against each fixed and random factor in the model. We selected models with the lowest Akaike information criterion (AIC) values and greater Akaike weights (Zuur & Ieno, 2016) and kept models within the AIC difference less than two from the best model.

Generalized linear mixed models (GLMM) were used in all analyses. Appendix Table A1 shows details of the error distributions, link functions, fixed and random factors for all analyses. To test for the effects of host plant treatment on postdiapause larval performance, we assessed development time, pupal weight, growth rate and survival to adulthood. Development time was calculated as the number of days each larva took from the seventh instar until pupation. The growth rate (g/day), from the seventh instar until pupation, was estimated by following the formula from Radford (1967). In the models for development time, pupal weight and growth rate, host plant treatment and sex were included as fixed factors and family as a random factor. In the model for survival to adulthood (1/0), we used seventh-instar weight instead of sex as a covariate, as the sex of the nonsurvivors was unknown. To assess whether the effect of developmental host plant treatment carried over to female reproductive performance, we assessed mating success (yes/no), oviposition success (yes/no), clutch size, lifetime egg production, hatching success (the proportion of eggs laid that hatched) and life span. For clutch size and hatching success, clutch rank (the order in which the mother oviposited the clutches) was additionally included as a fixed factor. To assess the effects of host plant treatment on the performance of the prediapause larvae, we assessed development time, weight at diapause and survival to diapause (number of larvae that reached diapause). We included offspring host plant treatment and maternal host plant treatment as fixed factors, and family and female ID nested within a family as random factors. We removed 75 larvae that skipped diapause from the analyses (in Finland skipping diapause is not an option for larvae in the wild). We also assessed with a chi-square test whether host plant treatment influenced the likelihood of larvae skipping diapause. All tested models are presented in Appendix Tables A2 and A3. Chi-square values and *P* values of all retained models are presented in Appendix Tables A4 and A5.

We used the difference in the leaf area eaten between the well-watered and the drought-exposed discs of host plants to determine the food preference of postdiapause larvae. This was tested using a GLMM with a Gaussian distribution where host plant treatment, trial number (1–3) and sex were included as fixed factors and family and larval ID as random factors. We also included second-order interactions in this model. We used statistical comparisons (multcomp R package; Hothorn, Bretz, & Westfall, 2008) to identify the effects of the fixed factors and a pairwise contrast to determine how means differed from each other. In the analysis of the oviposition host plant choice, we used a chi-square test for probabilities of oviposition on well-watered and drought-exposed plants (package stats, R Core Team, 2015). We fitted GLMM models with a binomial distribution (logit link function) to determine whether the oviposition host plant choice was influenced by host plant treatment and trial (1 and 2). Female ID was included as a random factor, and the second-order interaction was also added. Finally, we tested whether the host plant treatment of the female, the host plant choice or the trial influenced the clutch size. Here, we used a negative binomial distribution with log link function, with family and female ID nested within a family as random factors.

RESULTS

As the effect and significance of the fixed factors did not change in the alternative models (i.e. those within $\Delta\text{AIC} < 2$), we present

here only the results from the best models (i.e. those with the lowest AIC, Appendix Tables A1 and A2). Details of all models and results of the alternative models are presented in Appendix Tables A4 and A5. We present results in the order that the experiments were carried out.

Postdiapause Performance

Postdiapause larvae feeding on drought-exposed *P. lanceolata* host plant leaves developed faster, weighed more as pupae and consequently had a faster growth rate than larvae feeding on well-watered host plants (Table 1, Fig. 1). In general, males developed faster, weighed less as pupae and had a faster growth than females (Table 2). The seventh, and final, instar weight did not influence survival (Table 1).

In the analyses to assess food plant choice in the postdiapause larvae, we found a significant interaction between host plant treatment and trial (Table 1), indicating that only larvae fed with well-watered host plants developed a food preference towards drought-exposed leaf discs over time (i.e. trial number; Fig. 2). Based on a post hoc comparison it is evident that there was a clear food preference only in the last trial between the two treatment groups ($t = -2.46$; $P = 0.01$; see Appendix Table A6 for the multiple comparisons). The host plant treatment and the trial alone did not explain differences in the area eaten by the larvae (Table 1).

Adult and Prediapause Performance

The mating success (81%) and oviposition success (74%) were not influenced by the host plant treatment or by pupal weight (Table 3). Clutch size and lifetime egg production were not affected by the developmental treatment, whereas the hatching success of the eggs was influenced by the host plant treatment, the clutch rank and their interaction (Table 3). Females that were fed with well-watered host plants during their development had eggs with lower hatching success, especially in the later clutches compared with females fed with drought-exposed host plants during their development (Fig. 3a). In general, the number of eggs deposited as well as their hatching success decreased with clutch rank. Females that had been fed with well-watered host plants during their development also had poorer survival than females that had fed on drought-exposed host plants (Fig. 3b). Pupal weight did not influence lifetime egg production (Table 3).

Females showed an oviposition preference for well-watered host plants: 76% of the host plants females laid eggs on were from the well-watered group ($\chi^2 = 24.511$, $P < 0.001$). The oviposition choice was not explained by the female's own developmental host plant treatment. More eggs, in general, were laid in the first trial of each female (Table 3).

Table 1
Results of the best models for postdiapause life history traits and food preference

Traits	Factors	df	χ^2	<i>P</i>
Larval performance				
Development time	Host plant treatment	1	8.4	0.004
	Sex	1	7.3	0.007
Pupal weight	Host plant treatment	1	17.0	<0.001
	Sex	1	96.2	<0.001
Growth rate	Host plant treatment	1	29.5	<0.001
	Sex	1	17.0	<0.001
Survival to adulthood	Weight	1	0.3	0.609
Host plant preference				
Host plant area eaten	Host plant treatment	1	1.8	0.180
	Trial	2	3.7	0.157
	Host plant treatment*trial	2	6.8	0.033

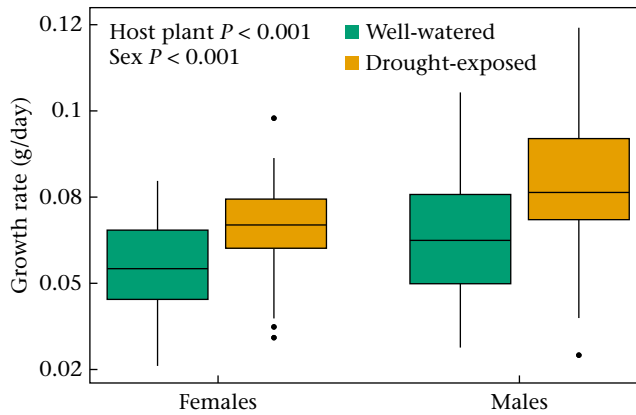


Figure 1. Effect of well-watered and drought-exposed host plant treatment on the growth rate of female and male postdiapause larvae. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

Table 2

Comparison of postdiapause larval and resulting female adult life history traits of individuals exposed to well-watered and drought-exposed host plants during their development

Life history traits	Sex	Well-watered		Drought-exposed	
		Mean (\pm SE)	N	Mean (\pm SE)	N
Postdiapause larvae					
Development time (days)	Female	15.0 (\pm 0.3)	43	13.7 (\pm 0.2)	47
	Male	13.8 (\pm 0.5)	39	11.7 (\pm 0.3)	37
Pupal weight (mg)	Female	159.1 (\pm 2.7)	43	170.0 (\pm 2.5)	47
	Male	135.6 (\pm 2.7)	40	143.7 (\pm 2.9)	37
Growth rate (g/day)	Female	0.05 (\pm 0.002)	43	0.07 (\pm 0.002)	47
	Male	0.06 (\pm 0.003)	39	0.08 (\pm 0.003)	37
Adults					
Clutch size	Female	130.9 (\pm 9.5)	51	141.0 (\pm 8.8)	53
Lifetime egg production	Female	267.1 (\pm 24.7)	25	311.5 (\pm 38.0)	24
Hatching success (%)	Female	87.7 (\pm 7.8)	51	91.3 (\pm 7.1)	53
Life span (days)	Female	14.8 (\pm 1.0)	28	16.8 (\pm 1.2)	30

Prediapause larval development time was not influenced by the type of food on which the larvae were fed (Table 3). Prediapause larvae feeding on drought-exposed host plants did, however, weigh less at diapause (Fig. 4a), and had 33% lower survival rate to diapause than larvae fed with well-watered host plants (Table 3). Additionally, a significant interaction between prediapause host plant treatment and the maternal host plant treatment on the survival of the larvae indicated that the prediapause larvae from mothers that had been feeding on drought-exposed plants during their development showed a milder impact of the drought-exposed treatment (Fig. 4b). Maternal developmental host plant treatment alone did not influence prediapause offspring survival (Table 3).

DISCUSSION

Nutritional and environmental conditions experienced during development can greatly impact the performance and fitness of individuals (Boggs, 2009; Lee, Kwon, & Roh, 2012; Monaghan, 2008; Nestel et al., 2016). As exposure to drought has been predicted to increase in intensity and frequency in the future (Bale et al., 2002; Morecroft et al., 2002), and precipitation is known to impact insect herbivores' population growth rates due to their effects on host plants (Kahilainen et al., 2018), we were explicitly interested here in how drought affects the performance of the herbivore larvae via the changes it induces in the host plants it feeds on. We were further interested in whether individuals can behaviourally adjust their own or their offspring's performance by choosing host plants that match their performance. Our results demonstrate that host plant drought greatly impacts life history variation and performance and that the responses depend on the developmental stage. The prediapause larval performance was reduced when feeding on drought-exposed host plants, whereas the effects were opposite at the postdiapause stage. The positive effect of feeding on drought-exposed host plants during the postdiapause stage even carried over to the adult stage as hatching success of the eggs and the life span of adult females were increased in females that had been feeding on drought-exposed

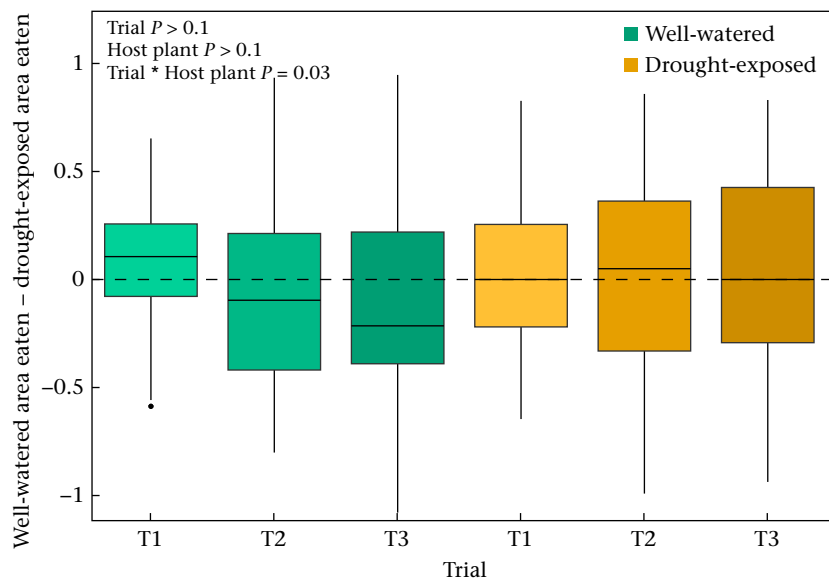


Figure 2. Diet preference of postdiapause larvae in the food choice test trial. Larvae were fed with host plants from either well-watered or drought-exposed host plants. Each individual was tested for 3 consecutive days (trials). The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circle is an outlier. Dashed line indicates no preference.

Table 3
Results of best models for adult life history, prediapause life history and adults' oviposition preference test

Traits	Factors	df	X ²	P
Adults				
Mating success	Pupal weight	1	2.5	0.118
Oviposition success	Host plant treatment	1	0.9	0.332
Clutch size	Host plant treatment	1	1.7	0.187
	Clutch rank	1	16.2 ¹	<0.001
Lifetime egg production	Pupal weight	1	3.1 ¹	0.077
Hatching success	Host plant treatment	1	133.36 ¹	<0.001
	Clutch rank	1	2407.16 ¹	<0.001
Life span	Host plant treatment * clutch rank	1	7.099 ¹	0.008
	Host plant treatment	1	4.9 ¹	0.027
Adults' oviposition preference				
Host plant choice	Host plant treatment	1	0.3	0.589
Clutch size	Trial	1	6.4 ¹	0.011
Prediapause larvae				
Development time	Host plant treatment	1	0.6	0.43
Weight at diapause	Host plant treatment	1	6.4	0.012
Survival to diapause	Host plant treatment	1	4.5	0.034
	Maternal host plant treatment	1	0.2	0.662
	Host plant treatment * maternal host plant treatment	1	11.45	<0.001

¹ Likelihood ratio test.

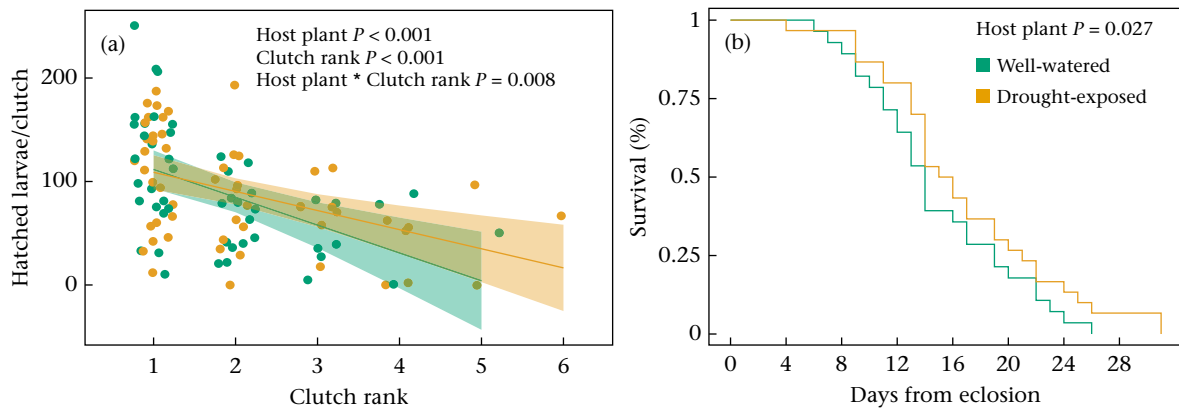


Figure 3. Adult life history trait responses to well-watered and drought-exposed host plant treatments. (a) Hatching success of eggs (regression line with 95% confidence intervals) and (b) female survival rate.

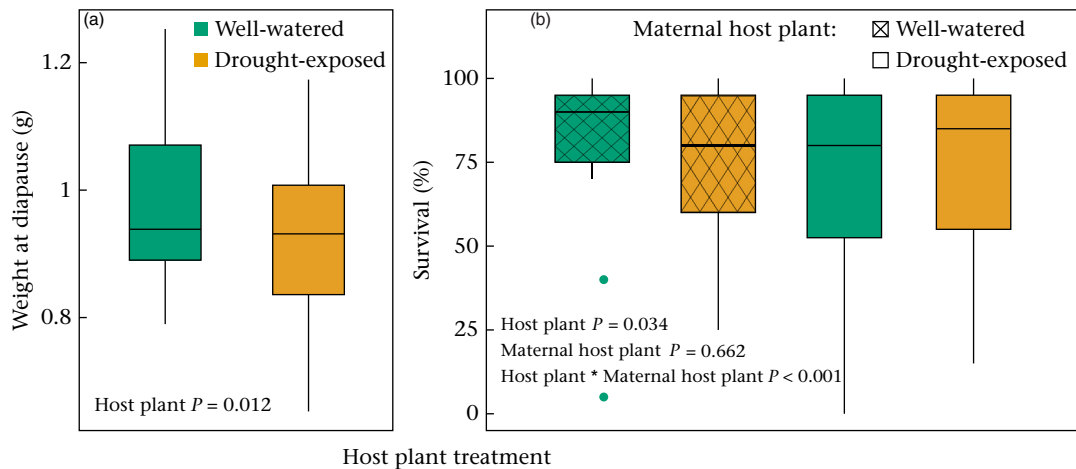


Figure 4. Effects of well-watered and drought-exposed host plant treatments on (a) weight at diapause and (b) survival rate of prediapause larvae. The box plots show the median and 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

host plants during their development. Additionally, we found behavioural adjustments at both the postdiapause and adult stages of the butterfly that increased their own and their young offspring's performance, respectively.

Responses to Drought-Exposed Host Plants are Stage Dependent

Plants respond to drought events by changes in morphology, physiology and chemistry (Showler & Moran, 2003). Plant exposure to stress may be beneficial to the herbivore feeding on them as, at least in some plants, stressful conditions have been shown to reduce the plants' availability of resources involved in herbivore resistance. Stressful conditions have been shown to increase the concentration of nutrients and/or decrease levels of secondary metabolites in the host plants (Jamieson et al., 2012; Mattson & Haack, 1987), resulting in increased performance, such as faster development time and increased body mass, of insects feeding on them (Gutbrodt et al., 2011). We found that even though the postdiapause larvae grew faster and the pupae weighed more when feeding on drought-exposed host plants, the prediapause larvae feeding on drought-exposed host plants were lighter at diapause and even had reduced survival. As the plants' responses to the treatment were not measured specifically, we can only speculate on the underlying mechanisms causing the observed differences. One may simply be the water status of the host plants. Even though plants that are exposed to drought often respond rapidly by closing stomata, increasing water uptake and reducing water loss, the prolonged exposure to drought in our experiment may have generated changes in the water profile of the host plants, thus increasing levels of nitrogen available for the herbivores and producing more nutritional plants to feed on, like those described above (Farooq et al., 2009; White, 1984). Differences in the response between the life stages may imply that the nutrition or nutritional balance differs between the developmental stages and that some of these core compounds were modified by the drought exposure in the plants. Consistent developmental stage-dependent responses have been shown in regard to secondary metabolites (*M. cinxia*; Saastamoinen, van Nouhuys, Nieminen, O'Hara, & Suomi, 2007) and proteins (*Manduca sexta*; Petersen, Woods, & Kingsolver, 2000). In *Papilio cressphontes*, final-instar larvae are less efficient at converting ingested food than the penultimate instar feeding on the same host plants (Scriber & Dowell, 2017). It is also possible that the underlying reasons for the stage-dependent responses involve not different nutritional requirements but more physical responses of the plants to the drought that may affect small and large larvae differently. In response to drought, plants often produce more sclerophyllous leaves (i.e. small, thick and tough; Chaves et al., 2003) which may be harder for young prediapause larvae to break and chew compared with the larger postdiapause larvae, preventing the former from reaching the nutrients that would otherwise be available to them. Physical defences, such as leaf toughness, are known to impact herbivore performance significantly, and they are indeed often the most important plant defences to deter herbivory (Massey & Hartley, 2009). The drought exposure of the host plants in the present study was relatively harsh and long (i.e. 12 weeks), giving the plants enough time to show these types of physical or chemical responses. Thus, milder drought exposure may alter the host plants differently and, consequently, the life history responses of the herbivore may also differ. Future work on the metabolite profiles and the physical responses of the host plant to different durations of drought are hence required to shed more light on the underlying mechanisms of the results obtained here.

Whatever the underlying mechanisms, the positive effects of feeding on drought-exposed host plants observed in the

postdiapause larvae were significant and carried over even to adult performance. Even though the number of eggs was not affected by the developmental conditions, the hatching success of the eggs laid and the adult life span of individuals fed with drought-exposed host plants during the postdiapause stage was increased compared to those fed with well-watered host plants. The increased hatching success of eggs in females that had been fed with drought-exposed host plants was more pronounced at an older age further supporting changes in adult senescence. These results are consistent with several other studies in Lepidoptera that have shown the importance of larval-derived reserves for life span (Boggs, 2002; Boggs & Freeman, 2005; Swanson et al., 2016). In the Glanville fritillary shortage of food during the postdiapause stage has also been shown to reduce fecundity or life span depending on the severity of the treatment (Saastamoinen et al., 2013). Developmental conditions experienced by the mothers may also impact the performance of the offspring (i.e. transgenerational effects; Woestmann & Saastamoinen, 2016), and such effects are presumed to be adaptive when the parents match their offspring phenotype to the environment the offspring will experience (Mousseau & Fox, 1998). We observed that the negative impact of drought-exposed host plants was milder in the prediapause larvae whose mother had also experienced drought-exposed host plants during their own development.

Preference–Performance in Larvae and Adults

The preference–performance hypothesis predicts that females will choose to oviposit their eggs on host plants that will increase the growth, survival and reproduction of their offspring (Gripenberg et al., 2010). Generally, variation in host plant use follows the abundance of the potential host species and their characteristics (age, size, primary and secondary metabolite concentrations and/or physical properties). Theory predicts that whenever there is a conflict between the life stages, the mothers should favour oviposition on host plants that are best for eggs and early stage offspring, even if the survival of later stages is better in other host plants (Thompson, 1988). Consistently, we found a strong preference for females to deposit eggs on well-watered host plants over drought-exposed host plants, which increased the performance of the prediapause but not the postdiapause larvae. The behavioural choice test experiment with the postdiapause larvae further showed that the larger larvae are themselves able to choose among the leaves exposed to different treatments.

Interestingly, the choosiness of individual postdiapause larvae towards the host plant that increased their own performance (i.e. drought-exposed host plant) became apparent only when the larvae had been fed with the host plant that generally resulted in reduced performance (i.e. well-watered host plant). This result further suggests that the well-watered host plants were lacking some nutrients that were important for the postdiapause larvae or that the nutrients were unbalanced and that only the larvae missing these nutrient/compounds chose the 'better quality diet'. This is consistent with studies that have shown that nutritional needs alter individual behaviour to feed on a diet with appropriate nutrients and/or to regulate their nutritional intake (Behmer, 2009; del Campo, Miles, & Caillaud, 2009; Jones & Agrawal, 2017). The behavioural choosiness observed in the present study increased with the exposure that individuals acquired over time (i.e. with successive trials), suggesting some form of sensitization (whereby with repeated exposure to a specific stimulus the individuals increase their response towards it; Jones & Agrawal, 2017; Papaj & Prokopy, 1989). Similar sensitization (a form of nonassociative learning) has been observed, for example, in the larvae of *M. sexta*: after repeated feeding on solanaceous host plants the individuals

become facultative specialists and stopped accepting other host plants (Anderson & Anton, 2014). Learning in insects generally improves foraging efficiency by decreasing the incidence of random food sampling, and consequently has a positive effect on fitness (Behmer, 2009; Jones & Agrawal, 2017).

Conclusions

Our work shows variation in response to changes in host plant quality along the life cycle of an insect herbivore, mediated by host plant responses to drought. These responses affected the development, fitness and survival, and even the behaviour, of the individuals. Very few studies so far have considered life history responses at different developmental stages within host plant species that vary in quality (but see Petersen et al., 2000; Rodrigues et al., 2015; Saastamoinen et al., 2007). Our results on the increased performance of postdiapause larvae on drought-exposed plants suggest that the general preference of the Glanville fritillary for sites with warmer microclimatic conditions may be due not solely to warmer thermal conditions but also, at least partially, to the changes in host plant quality. Future studies should aim to identify the underlying mechanisms that cause stage-dependent variation in the responses, as possibilities include both nutritional and physical modifications in the plants due to drought stress.

Acknowledgments

We thank Brandon Meter, Carolina Sánchez Carpena, Samuli Hapalainen and Suvi Ikonen for their assistance during the experiments. We acknowledge Aapo Kahilainen, Dimitri Stucki, Elena Rosa, Luisa Woestmann, Michelle Dileo, Elina Numminen, Rose Thorogood and two anonymous referees for their help with data analyses and comments on the manuscript. This work was supported by the European Research Council (Independent starting grant no. 637412 'META-STRESS' to M.S.) and by Lammi Biological Station grant (to A.S.). We declare that we have no conflict of interest.

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Appendix

Table A1

Model description including the error distribution, link function, fixed factors and random factors for each of the full models

Life history traits	Distribution	Link function	Fixed factors		Random factors		
Postdiapause larvae	Poisson	Log	Treatment	Sex	Family		
Development time (days)	Gaussian	Identity	Treatment	Sex	Family		
Pupal weight (mg)	Gaussian	Identity	Treatment	Sex	Family		
Growth rate (g/day)	Binomial	Logit	Treatment	7th instar weight	Family		
Survival to adulthood							
Adults							
Mating success	Binomial	Logit	Treatment	Pupal weight	Family		
Oviposition success	Binomial	Logit	Treatment	Pupal weight	Family		
Clutch size (eggs/clutch)	Negative binomial	Log	Treatment	Clutch rank	Family		
Lifetime egg production	Negative binomial	Log	Treatment	Pupal weight	Family		
Hatching success	Binomial	Logit	Treatment	Clutch rank	Family		
Life span (days)	Poisson	Log	Treatment	Pupal weight	Family		
Prediapause larvae							
Development time (days)	Gaussian	Identity	Treatment	Maternal treatment	Family	Female ID/Family	
Weight at diapause (mg)	Gaussian	Identity	Treatment	Maternal treatment	Family	Female ID/Family	
Survival to diapause	Binomial	Logit	Treatment	Maternal treatment	Family	Female ID/Family	
Postdiapause food preference							
Host plant area eaten	Gaussian	Identity	Treatment	Trial	Sex	Family	Larval ID/Family
Adult's oviposition choice							
Host plant choice	Binomial	Logit	Treatment	Trial	Maternal treatment	Family	Female ID/Family
Clutch size	Negative binomial	Log	Treatment	Trial			

Table A2

List of all models tested for each life history trait

Life history traits	Model	Fixed effects	Random effects	df	AIC	ΔAIC	Akaike weights
Postdiapause larvae							
Developmental time	1	Host plant treatment*sex	Family	5	796.794	1.324	0.311
	2	Host plant treatment+ sex	Family	4	795.471	0	0.642
Pupal weight	3	Host plant treatment	Family	3	800.841	5.37	0.042
	4	Sex	Family	3	801.866	6.395	0.025
	5	Host plant treatment*sex	Family	6	-95.821	5.9	0.049
	6	Host plant treatment+ sex	Family	5	-99.963	0	0.94
	7	Host plant treatment	Family	4	-31.549	68.414	0
	8	Sex	Family	4	-91.301	8.663	0.011
Growth rate	9	Host plant treatment*sex	Family	6	-846.931	10.089	0.006
	10	Host plant treatment+ sex	Family	5	-857.02	0	0.883
	11	Host plant treatment	Family	4	-841.89	4.152	0.111
Survival to adulthood	12	Sex	Family	4	-841.89	15.129	0
	13	Host plant treatment*weight	Family	5	318.561	3.812	0.062
	14	Host plant treatment+ weight	Family	4	316.75	2	0.154
	15	Host plant treatment	Family	3	315.011	0.262	0.366
	16	Weight	Family	3	314.75	0	0.418
Adults							
Mating success	17	Host plant treatment*pupal weight	Family	5	81.665	0.589	0.29
	18	Host plant treatment+ pupal weight	Family	4	82.361	1.286	0.204
	19	Host plant treatment	Family	3	83.477	2.401	0.117
	20	Pupal weight	Family	3	81.076	0	0.389
Oviposition success	21	Host plant treatment*pupal weight	Family	5	81.446	1.106	0.219
	22	Host plant treatment+ pupal weight	Family	4	82.1	1.76	0.158
	23	Host plant treatment	Family	3	80.34	0	0.381
Clutch size	24	Pupal weight	Family	3	81.248	0.908	0.242
	25	Host plant treatment*clutch rank	Family	6	1165.556	1.191	0.355
	26	Host plant treatment+ clutch rank	Family	5	1164.365	0	0.645
	27	Host plant treatment	Family	3	3778.379	2614.014	0
Lifetime egg production	28	Clutch rank	Family	3	3172.298	2007.933	0
	29	Host plant treatment*pupal weight	Family	6	634.41	3.656	0.084
	30	Host plant treatment+ pupal weight	Family	5	632.588	1.835	0.209
	31	Host plant treatment	Family	4	632.834	2.081	0.185
Hatching success	32	Pupal weight	Family	4	630.754	0	0.523
	33	Host plant treatment+ clutch rank	Family	5	5336.942	0	0.928
	34	Host plant treatment+ clutch rank	Family	4	5342.04	5.099	0.072
	35	Host plant treatment	Family	3	7747.201	2410.259	0
Life span	36	Clutch rank	Family	3	5473.4	136.458	0
	37	Host plant treatment*pupal weight	Family	5	392.207	2.785	0.135
	38	Host plant treatment+ pupal weight	Family	4	391.109	1.687	0.233
	39	Host plant treatment	Family	3	389.422	0	0.542
40	Pupal weight	Family	3	393.012	3.59	0.09	
Prediapause larvae							
Development time	41	Host plant treatment*maternal host plant treatment	female ID/family	7	383.4	2.487	0.11
	42	Host plant treatment+ maternal host plant treatment	female ID/family	6	383.011	2.098	0.134
	43	Host plant treatment	female ID/family	5	380.913	0	0.382
	44	Maternal host plant treatment	female ID/family	5	380.956	0.043	0.374
Weight at diapause	45	Host plant treatment*maternal host plant treatment	female ID/family	7	-109.229	10.473	0.004
	46	Host plant treatment+ maternal host plant treatment	female ID/family	6	-115.184	4.517	0.077
	47	Host plant treatment	female ID/family	5	-119.702	0	0.734
	48	Maternal host plant treatment	female ID/family	5	-116.949	2.752	0.185
Survival to diapause	49	Host plant treatment*maternal host plant treatment	female ID/family	6	568.818	0	0.966
	50	Host plant treatment+ maternal host plant treatment	female ID/family	5	578.122	9.304	0.009
	51	Host plant treatment	female ID/family	4	576.315	7.497	0.023
	52	Maternal host plant treatment	female ID/family	4	580.794	11.976	0.002

The best model for each trait after Akaike information criterion (AIC) analysis is marked in bold.

Table A3

List of all models tested on host plant preference

Type of choice	Model	Fixed effects	Random effects	df	AIC	ΔAIC	Akaike weights
Postdiapause food choice							
Difference in area of host plant eaten	1	Host plant treatment*trial*sex	Larva ID/family	15	594.572	27.323	0
	2	Host plant treatment*trial + sex	Larva ID/family	10	573.664	6.415	0.032
	3	Host plant treatment + trial + sex	Larva ID/family	8	570.147	2.899	0.184
	4	Host plant treatment*trial	Larva ID/family	9	567.249	0	0.784
Adults' oviposition choice							
Host plant type	5	Host plant treatment*trial	Female ID/family	6	159.116	3.959	0.058
	6	Host plant treatment + trial	Female ID/family	5	157.152	1.994	0.155
	7	Host plant treatment	Female ID/family	4	155.157	0	0.421
	8	Trial	Female ID/family	4	155.446	0.289	0.365
Clutch size	9	Host plant treatment*Maternal host plant treatment*trial	Family	10	898.079	9.84	0.004
	10	Host plant treatment*Maternal host plant treatment + trial	Family	7	892.972	4.732	0.049
	11	Host plant treatment + Maternal host plant treatment + trial	Family	6	891.534	3.294	0.101
	12	Host plant treatment*Maternal host plant treatment	Family	6	897.634	9.395	0.005
	13	Maternal host plant treatment*trial	Family	6	891.95	3.71	0.082
	14	Host plant treatment*Maternal host plant treatment	Family	5	895.889	7.649	0.011
	15	Maternal host plant treatment + trial	Family	5	889.956	1.717	0.223
	16	Trial	Family	4	888.24	0	0.525

The best model after Akaike information criterion (AIC) analysis marked in bold.

Table A4

Results of all top models for the life history traits (i.e. those that presented AIC value differences less than two units from the best model)

Life history traits	Model	AIC	Factors	df	X ²	P	Variance estimates	SD
Postdiapause larvae								
Development time	2	795.471	Host plant treatment	1	8.384	0.004	0	0
			Sex	1	7.335	0.007		
Pupal weight	6	-99.963	Host plant treatment	1	17.034	<0.001	0.004	0.066
			Sex	1	96.203	<0.001		
			Family					
			Residual					
Growth rate	10	-857.020	Host plant treatment	1	29.540	<0.001	0.025	0.159
			Sex	1	17.034	<0.001		
Survival to adulthood	16	314.750	Weight	1	0.261	0.609	0	0
			Family					
	15	315.011	Host plant treatment	1	0	0.995	0	0
			Family					
	14	316.750	Host plant treatment	1	0	0.995	0	0
			Weight	1	0.261	0.609		
Family								
Adults								
Mating success	20	81.076	Pupal weight	1	2.449	0.118	0	0
			Family					
	17	81.665	Host plant treatment	1	0.308	0.579	0	0
			Pupal weight	1	2.205	0.138		
18	82.361	Host plant treatment*pupal weight	1	2.381	0.123	0	0	
		Family						
Oviposition success	23	80.34	Host plant treatment	1	0.942	0.332	0	0
			Family					
	24	81.248	Pupal weight	1	0.058	0.809	0	0
			Family					
	21	81.446	Host plant treatment	1	0.824	0.364	0	0
			Pupal weight	1	0.241	0.624		
22	82.1	Host plant treatment*pupal weight	1	2.536	0.111	0	0	
		Family						
Clutch size	26	1164.365	Host plant treatment	1	1.744 ¹	0.187	0.006	0.0804
			Clutch rank	1	16.227 ¹	<0.001		
25	1165.556	Host plant treatment	1	1.744 ¹	0.187	0.005	0.067	
		Clutch rank	1	16.227 ¹	<0.001			
		Host plant treatment*clutch rank	1	0.809 ¹	0.368			
Family								

(continued on next page)

Table A4 (continued)

Life history traits	Model	AIC	Factors	df	X ²	P	Variance estimates	SD		
Lifetime egg production	32	630.754	Pupal weight Family	1	3.127 ¹	0.077				
	30	632.588	Host plant treatment Pupal weight Family	1	0.165 ¹	0.684	<0.001	<0.001		
Hatching success	33	5336.942	Host plant treatment	1	133.360 ¹	<0.001				
			Clutch rank	1	2407.160 ¹	<0.001				
			Host plant treatment*clutch rank Family	1	7.099 ¹	0.008	<0.001	0.450	0.671	
Life span	39	389.422	Host plant treatment Family	1	4.901 ¹	0.027	0.017	0.133		
	38	391.109	Host plant treatment Pupal weight Family	1	3.903 ¹	0.048				
Prediapause larvae Development time	43	380.913	Host plant treatment	1	0.622	0.43	0.674	0.821		
			Female ID Family Residuals				0	0	1.985	1.409
Weight at diapause	47	-119.702	Maternal host plant treatment Female ID Family Residuals	1	0.048	0.827	0.715	0.846		
			Host plant treatment Female ID Family Residuals				0	0	1.969	1.403
			Host plant treatment Female ID Family Residuals	1	6.356	0.012	0.002	0.001	0.011	0.047
Survival to diapause	49	568.818	Host plant treatment	1	4.480	0.034				
			Maternal host plant treatment	1	0.190	0.662				
			Host plant treatment*maternal host plant treatment Female ID Family	1	11.479	<0.001	1.393	1.180		
						0.035	0.187			

The models are presented starting from the lowest AIC value.

¹ Likelihood ratio test.

Table A5

Results of all top models for the choice tests (i.e.: those that presented AIC value differences less than two units from the best model)

Preference	Model	AIC values	Factors	df	X ²	P	Variance estimates	SD		
Postdiapause Host plant area eaten	4	567.249	Host plant treatment	1	1.798	0.180				
			Trial	2	3.709	0.157				
			Host plant treatment*trial	2	6.834	0.033				
			Larva ID Family Residuals				0.003	0	0	0.056
							0.164	0.405		
Adults' oviposition Host plant choice	7	155.157	Host plant treatment	1	0.292	0.589	<0	<0		
			Female Family				0	0		
	8	155.446	Trial	1	0.003	0.958	0	0		
			Female ID Family				0	0		
	6	157.152	Host plant treatment	1	0.294	0.587	0	0		
			Trial	1	0.006	0.941	0	0		
Clutch size	16	888.240	Host plant treatment	1	6.436 ¹	0.011	0.003	0.055		
			Female Family				0	0		
			Maternal host plant treatment	1	0.283 ¹	0.595				
15	889.956	Trial	1	6.336 ¹	0.012					
		Family				0.002	0.046			

The models are presented starting from the lowest AIC value.

¹ Likelihood ratio test.

Table A6

Multiple comparisons of means in the post hoc analysis for the food choice test of the postdiapause larvae

Group	Estimate	SE	Z	P
Well-watered 1 – Well-watered 2	0.156	0.063	2.493	0.067
Well-watered 1 – Well-watered 3	0.187	0.063	2.997	0.015
Well-watered 2 – Well-watered 3	0.031	0.063	0.504	0.983
Drought-exposed 1 – Drought-exposed 2	-0.020	0.063	-0.327	0.997
Drought-exposed 1 – Drought-exposed 3	-0.030	0.063	-0.484	0.985
Drought-exposed 2 – Drought-exposed 3	-0.010	0.063	-0.157	0.999

The number after the host plant treatment refers to the trial.