

ORIGINAL ARTICLE

Development on drought-stressed host plants affects life history, flight morphology and reproductive output relative to landscape structure

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Abstract

With global climate change, rainfall is becoming more variable. Predicting the responses of species to changing rainfall levels is difficult because, for example in herbivorous species, these effects may be mediated indirectly through changes in host plant quality. Furthermore, species responses may result from a simultaneous interaction between rainfall levels and other environmental variables such as anthropogenic land use or habitat quality. In this eco-evolutionary study, we examined how male and female *Pararge aegeria* (L.) from woodland and agricultural landscape populations were affected by the development on drought-stressed host plants. Compared with individuals from woodland landscapes, when reared on drought-stressed plants agricultural individuals had longer development times, reduced survival rates and lower adult body masses. Across both landscape types, growth on drought-stressed plants resulted in males and females with low forewing aspect ratios and in females with lower wing loading and reduced fecundity. Development on drought-stressed plants also had a landscape-specific effect on reproductive output; agricultural females laid eggs that had a significantly lower hatching success. Overall, our results highlight several potential mechanisms by which low water availability, via changes in host plant quality, may differentially influence *P. aegeria* populations relative to landscape structure.

Introduction

Current climate change scenarios predict a global increase in temperature, spatial heterogeneity in precipitation, UV-B penetration and extreme events such as drought (Bale et al. 2002). Rainfall is becoming more variable, changing not only in quantity but also in severity and seasonality (Menzel et al. 2006), and it has been suggested that in some parts of Europe, summer droughts will become increasingly frequent (Morecroft et al. 2002). Predicting the ecological response of species to variation in rainfall levels is difficult as little research has been published documenting the direct effects of changing rainfall levels on species abundance and distribution (Bale et al.

2002). Also, to further complicate matters, the effects of changing rainfall levels are often actually mediated indirectly, for example in herbivorous insect species via changes in host plant quality (e.g. Stefanescu et al. 2004; Talloen et al. 2004; Turlure et al. 2010). Although in principle the patterns of response of species to changing rainfall levels can be detected globally, eco-evolutionary mechanisms underlying these responses operate locally at the level of individuals and populations and may result from a simultaneous interaction with other environmental variables such as anthropogenic land use or habitat quality (Stefanescu et al. 2004; Schweiger et al. 2006). Ecological studies have recently recognized that rapid rates of evolution are possible within species, with consequences

for species abundance and distribution (e.g. Sgro et al. 2011). For example, within the same climatic zone, populations occupying habitats in open areas are more likely to be exposed to short-term, intensive drought than those in forest or woodland areas (Sota and Mogi 1992). Given that the life history and reproductive strategies of individuals within a population are dependent on the prevailing environmental conditions (Roff 1992; Stearns 1992), such spatial and temporal heterogeneity in water availability may influence life-history evolution and population dynamics (e.g. Sota and Mogi 1992). Examining species eco-evolutionary responses to the interaction between climate-driven changes in water availability and anthropogenic land use has an applied significance for conservation and landscape management strategies (Sgro et al. 2011). A greater understanding of these interactions is essential for making reliable and accurate predictions of species' current and future ranges and for ensuring that populations are resilient in the face of continued climate change (Sgro et al. 2011).

Our model species, the speckled wood butterfly (*Pararge aegeria* L.), is primarily a woodland landscape butterfly, but in north-west Europe this species has colonized agricultural landscapes containing small, widely distributed 'woodland' fragments along hedgerows (Dover and Sparks 2000; Merckx et al. 2003). *Pararge aegeria* tend to require humid, semi-shaded conditions for optimal larval growth (Shreeve 1986; Pollard 1988). In woodland populations, variation in rainfall levels significantly contributes to variation in adult body mass in nature (Gibbs et al. 2011a,b), and from laboratory experiments we know that growth on drought-stressed plants results in longer development times, smaller adult masses and reduced forewing melanization because of the low nitrogen, water and carbon content of leaves (Talloe et al. 2004). Previous studies by Pollard (1988) and Schweiger et al. (2006) observed that distribution and abundance patterns of *P. aegeria* differed significantly between humid and dry years and that there was an interaction effect of habitat quality. The colonizing potential of *P. aegeria* was found to be restricted under arid conditions, and individuals in open, less thermally buffered habitats (e.g. in agricultural landscapes) were particularly affected (Schweiger et al. 2006). These data suggest that *P. aegeria* populations occupying woodland and agricultural landscapes are differentially affected by low water availability, but currently the mechanisms underlying these population-specific responses are not yet understood. Compared with individuals from woodland landscapes, individuals from fragmented agricultural landscapes have heavier adult body masses (Merckx and Van Dyck 2006; Merckx et al. 2006), suggesting higher resource investment into body mass during larval growth. Given their heavier adult body

masses, we hypothesized that larval growth on drought-stressed plants would carry a higher cost for individuals of agricultural origin than for individuals of woodland landscape origin, with drought stress constraining their investment in adult body mass, forewing melanization, flight morphological traits (wing loading and forewing aspect ratio) and reproduction (female fecundity and egg-hatching success). Using *P. aegeria* from populations from differently fragmented landscapes, we tested this hypothesis by rearing individuals in a common garden environment in the laboratory under two different growth conditions: (i) control and (ii) drought-stressed plants of the grass species *Poa trivialis*. We predicted that (i) growth on drought-stressed plants would result in prolonged development times and reduced survival from egg to adult and result in adults with lighter body masses and lower forewing melanization, forewing aspect ratio and wing loading, (ii) the observed lengthening of development and decline in adult mass, forewing melanization, forewing aspect ratio and wing loading would be larger for agricultural individuals (i.e. there will be a significant landscape by host plant treatment interaction effect), (iii) because females have heavier body masses than males and are more adversely affected by nutrient stress than males (Gibbs et al. 2004, 2006), the observed lengthening of development and decline in adult mass, forewing melanization, forewing aspect ratio and wing loading would be larger for females (i.e. there will be a significant sex by host plant treatment interaction effect) and (iv) compared with woodland females, agricultural females would have reduced investment in reproduction resulting in lower fecundity and reduced egg-hatching success (i.e. there will be a significant landscape by host plant treatment interaction effect).

Materials and methods

Study species

Pararge aegeria are temperate zone butterflies that lay eggs singly on grass species from the family Poaceae (Shreeve 1986). Females mate soon after emergence and usually mate only once (Wickman and Wiklund 1983). At eclosion they have no (Karlsson 1987) or only a few (8–24; Bink 1992) mature oocytes, and if mated on the day of emergence, they usually start ovipositing 48 h later on the third day of their adult life (Gibbs and Van Dyck 2010; Gibbs et al. 2010a,b). *Pararge aegeria* egg-laying site temperatures range between 17 and 30°C (Shreeve 1986), and experiments have shown that both agricultural and woodland females lay eggs within this temperature range (Karlsson and Van Dyck 2005). As such, for our experiments we chose an intermediate temperature of 24°C for oviposition and larval development. In female *P. aegeria*,

resources for reproduction are, to a significant degree, obtained during the larval stage and there is little opportunity to obtain more nitrogenous resources for reproduction through adult feeding (Karlsson 1994) or nuptial gifts (Svård and Wiklund 1989). Nutrient stress during larval growth prolongs development and results in lighter, small-sized *P. aegeria* adults at eclosion, and females are more adversely affected than males (Gibbs et al. 2004, 2006). A preliminary study of the wing pigments of *P. aegeria* identified that melanins are the major pigments for basal forewing darkness (Talloe et al. 2004), and forewing melanization is known to be important for *P. aegeria* thermoregulation; individuals with darker wings heat up more quickly than individuals with paler wings and consequently have more time available for activities associated with mate location and oviposition under cooler conditions (Van Dyck and Matthysen 1998; Berwaerts et al. 2001).

Host plant treatment

Potted host plants of *P. trivialis* were grown under standard conditions from commercially produced seed provided by Limagrain Advanta Belgium, and each plant was watered via its own individual water tray. At maturation the plants were randomly assigned to one of two treatment groups: control or drought-stressed. Control plants were watered daily with rain water both prior to the start of the experiment (i.e. 20 days before larval hatching) and throughout the experimental period (i.e. during larval development). Control plants were watered daily to prevent their soil from drying out (and the plant from wilting), but the soil was never oversaturated with water. Drought-stressed plants were deprived of water for 20 days prior to the start of the experiment and then were subsequently only provided with rain water once every 6 days throughout the experimental period. By only watering the plants every 6 days, we ensured that the plants remained alive (and had leaves available for larval consumption) but experienced moderate drought stress throughout the experimental period (after Talloe et al. 2004).

Larval life history

Newly hatched larvae were randomly selected and collected from four different outbred laboratory stock populations that originated from two different landscape types (cf. Merckx et al. 2003) in Belgium: two populations from a deciduous woodland landscape (Lauzelle and St. Hubert) and two populations from an agricultural landscape (Lillois and Hoegaarden). The larvae were placed (three per plant and all originating from the same

laboratory source population) on potted host plants of *P. trivialis* (either control or drought-stressed) and reared in a climate room in common garden conditions ($24 \pm 2^\circ\text{C}$ day, $16 \pm 2^\circ\text{C}$ night, LD 16:8) until eclosion. As a higher mortality was expected with drought stress (see Talloe et al. 2004), a total of 178 and 390 larvae were assigned to the control and drought stress treatment groups, respectively, and each laboratory source population contributed equivalent numbers of larvae to each treatment group. The rearing pots were spatially randomized with respect to population of origin and host plant treatment group.

Each individual larva was monitored throughout development. When a prepupa was observed, it was removed (still suspended on a blade of grass) and placed into an individual labelled container. Date of eclosion was recorded, and total development time was calculated (i.e. the number of days between hatching and eclosion as an adult). Mean egg-to-adult survival was calculated per population.

Female fecundity and egg-hatching success

On the day of eclosion, F_1 generation adults were weighed on an Ohaus Explorer balance (accuracy: 0.1 mg) and sexed. Females were then randomly chosen and placed individually in netted cages (0.5 m^3) along with a potted *P. trivialis* (from the control treatment group) for oviposition and an artificial flower containing a 10% honey solution (for design see Cory and Goulson 1993). *Pararge aegeria* adults actively feed from artificial flowers, and this feeding method has been routinely adopted in laboratory experiments; the honey solution was replenished daily (e.g. Gibbs et al. 2005, 2010a,b). Later the same day (between 13 and 16 h) a 1-day-old randomly chosen nonsibling male (originating from the same laboratory source population and reared on control plants) was introduced to the cage and, after mating, the pair was left undisturbed for 24 h. When the first egg was laid, the male was removed from the cage (and sacrificed for morphological measurements; see below) and the female was left to continue egg laying until death. The number of days between the introduction of the male and the first egg being laid was recorded for each female and used as a measure of time to onset of oviposition. In total, 100 females (50 of woodland landscape of origin and 50 of agricultural landscape of origin) were thus set up.

Every third day all cages were inspected for eggs. Eggs laid by each female were collected and counted. The total number of eggs laid was calculated for each female and used in analyses as a measure of lifetime realized fecundity (after Gibbs et al. 2010a,b). For each female, the

same oviposition plant was used throughout the duration of the experiment.

Pararge aegeria eggs are spherical, and the size of each egg could therefore be measured as a cross-sectional projection (mm^2) using a digital camera (Canon A720 IS, Canon Ltd., Reigate, UK). The resulting images were then measured using Image J 1.38x (freely available at <http://rsb.info.nih.gov/ij/>). This method is a highly reliable measure of egg size in *P. aegeria* as there is a strong correlation between egg area and egg mass in this species (cf. Bauerfeind and Fischer 2008). For each female, we determined the total number of eggs laid during her life and calculated the mean size of all of those eggs. All of the eggs laid by each female were kept and used to monitoring larval hatching. The proportion of eggs that hatched successfully was recorded for each female, and all females laid some viable eggs.

Longevity was recorded as the number of days from eclosion as an adult to death. Upon death, female wing morphological traits were measured, and any females with damaged wings were excluded from the analyses (see below).

All of the other adult males and females that eclosed, but were not used in this breeding experiment, were killed by freezing and stored at -20°C until their morphological measurements were taken.

Adult wing morphology measurements

Fore- and hindwings were carefully removed from the thorax and placed underneath a glass microscope slide. Digital images were then taken of the dorsal wing surface using a Nikon D1 Digital SLR (105 mm 1:4.5 UV Nikkor lens, Nikon Ltd., Kingston upon Thames, UK) under carefully controlled light conditions (i.e. F11, 1/125 shutter speed and a microtec fibre optics MFO-90 ring light). Using these digital pictures, the flight morphological traits, forewing surface area (mm^2), hindwing surface area (mm^2), forewing length (mm) and forewing melanization, were measured using the image analysing software Image J 1.38x (freely available at <http://rsb.info.nih.gov/ij/>). The degree of basal melanization of each dorsal forewing was quantified as the average grey value (scaled from 0, i.e. black, to 255, i.e. white) of the area of the discal wing cell (cf. Talloen et al. 2004). Wing loading was calculated as total body weight / total wing area (cf. Betts and Wootton 1988; Breuker et al. 2010). Mean forewing length and mean forewing surface area were determined for each individual, and these measures were used to calculate forewing aspect ratio: $\text{forewing length}^2/\text{forewing area}$ (cf. Betts and Wootton 1988; Breuker et al. 2010). For each trait measured, damaged wings were excluded from analyses. Based on repeat measurements of

a random subset of 30 individuals, the amount of measurement error because of imaging and digitizing was negligible (forewing length repeatability = 95.2%, $P < 0.0001$ and wing surface area measures repeatability = 99.95%, $P < 0.0001$).

Statistical analyses

General linear mixed models (GLMMs) were fitted to explain the variation in the following traits: larval development time, adult mass at eclosion, wing loading, forewing melanization, forewing aspect ratio, female fecundity and egg-hatching success. In all of these models, the fixed factors were landscape type, sex and plant treatment, with the exception of the models for fecundity and egg-hatching success, where sex was not included. Two different populations were sampled per landscape type to provide a level of repeatability at the landscape level. Population nested within landscape was thus used as a random factor in all models, and the *F*-ratio for the fixed-effect landscape is calculated as the ratio of the variation between landscapes to the variation within landscapes. The error variance in calculating the *F*-ratios for the other fixed effects (i.e. sex and host plant treatment) and the random effect of population was the model error variance.

Interaction effects between all of the fixed effects were tested, including the three-way interactions. For example, larval growth on drought-stressed plants was expected to prolong development time, in particular in agricultural females (predictions 1, 2 and 3 combined). Using a backward elimination procedure, only significant (i.e. $P < 0.05$) interaction effects were included in the final model. Where it was appropriate to include them, covariates were tested, but only significant covariates were included in the final model after backward elimination. Covariates tested included development time in GLMMs for adult mass and wing traits and mean egg size, female longevity and egg number in GLMMs for fecundity.

Residuals were examined for linearity and normality by inspecting normal probability plots and histograms of the residuals and by plotting the residuals versus the predicted values. Larval development time was transformed by taking the square root as the residual analyses showed it to have a moderate positive skew (i.e. a small number of caterpillars took a long time to develop). The arcsine square root of the percentage of eggs that hatched successfully was taken as there was a very strong negative skew (i.e. very few eggs hatched of a small number of females).

A linear mixed effect (LME) model with a logit link function and binomial error distribution (i.e. logistic regressions with random effects) was used to analyse variation in survival (0 = dead, 1 = alive) from egg hatching

to eclosion as an adult. Population nested within landscape was used as a random effect, while landscape and treatment were used as fixed effects. Sex was not included as individuals that did not survive the larval stages could not be sexed. As the overdispersion parameter (by which P -values and confidence intervals should be adjusted for overdispersion) was never significantly different from 1, overdispersion correction did not alter the model output and thus was not reported here.

Analyses were performed both in R 2.10.1 (packages nlme and lme4; <http://lib.stat.cmu.edu/R/CRAN/>) and in Statistica 9.1 with R functionality (Statsoft Ltd., Milton Keynes, UK)

Results

Table 1 summarizes averages for the following traits: larval development time, adult mass, forewing melanization, forewing aspect ratio, wing loading, lifetime female fecundity, female longevity, mean lifetime egg size and mean egg-hatching success across each of the four treatment groups.

Larval development time and adult mass

Larval growth on drought-stressed plants was predicted to prolong development time and reduce adult mass, in particular in agricultural females (predictions 1, 2 and 3).

The effect of drought stress on larval development time was dependent on the landscape of origin (significant landscape by host plant treatment effect, $F_{1,447} = 16.50$, $P < 0.001$; no main effect of landscape type, $F_{1,2.59} = 5.70$, $P = 0.11$, nor of host plant treatment, $F_{1,447} = 2.90$, $P = 0.089$). Compared with the larvae from each of the other treatment groups, agricultural larvae reared on drought-stressed plants had significantly longer development times (Fig. 1). Females took longer to develop than males (mean \pm SE females = 31.65 ± 0.18 , males = 28.82 ± 0.12 ; $F_{1,447} = 198.50$, $P < 0.001$), but

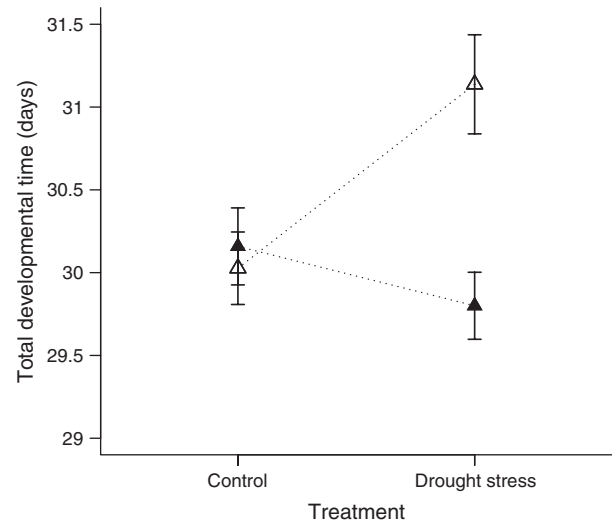


Figure 1 Mean total development time (\pm SE) for individuals from woodland (closed triangles, both populations pooled) and agricultural landscapes reared (open triangles, both populations pooled) on control and drought-stressed host plants.

there were no significant interaction effects between sex, treatment and landscape. There was no significant variation amongst the populations within a landscape ($F_{1,447} = 1.10$, $P = 0.33$).

Development time in turn explained a significant part of the variation in mass upon eclosion, with animals that developed for longer being lighter (slope parameter for covariate development time in GLMM = -2.27 , $F_{1,443} = 109.07$, $P < 0.001$). Variation between landscapes was smaller than between the populations within landscapes (fixed effect of landscape, $F_{1,2.02} = 0.096$, $P = 0.78$; random effect of population, $F_{2,443} = 35.95$, $P < 0.001$, which accounted for 6.9% of the total variation). However, the effect of host plant treatment on adult mass is dependent upon both the sex of the individuals and the landscape type (three-way interaction: $F_{4,443} = 4.70$, $P = 0.0010$; Figs 2 and 3). Females were

Table 1. Mean trait values (\pm SE) for *P. aegeria* individuals from woodland and agricultural landscapes reared on control and drought-stressed *P. trivialis* host plants.

Trait	Agricultural landscape		Woodland landscape	
	Control	Drought stress	Control	Drought stress
Total development time (days)	30.02 (0.22)	31.14 (0.30)	30.16 (0.23)	29.80 (0.20)
Adult mass (mg)	63.74 (1.38)	51.20 (1.49)	61.10 (1.50)	56.44 (0.98)
Forewing melanization	56.43 (0.82)	54.80 (0.66)	55.21 (0.82)	56.32 (0.51)
Forewing aspect ratio	1.75 (0.004)	1.74 (0.004)	1.76 (0.004)	1.74 (0.002)
Wing loading (mg/mm ²)	0.09 (0.002)	0.08 (0.002)	0.09 (0.002)	0.09 (0.002)
Female fecundity	133.42 (8.21)	111.95 (10.18)	133.77 (9.75)	125.12 (9.46)
Egg-hatching success	0.72 (0.03)	0.61 (0.05)	0.71 (0.03)	0.76 (0.02)
Female longevity	14.36 (0.83)	15.50 (0.92)	13.87 (0.53)	14.56 (0.78)

significantly bigger than males (mean \pm SE females = 64.12 ± 0.99 , males = 50.79 ± 0.68 ; main effect of sex, $F_{1,443} = 296.61$, $P << 0.001$), drought stress resulted in lighter individuals ($F_{1,443} = 64.88$, $P << 0.001$), but females suffered greater reductions in mass, and in males the mass reductions were more severe in the agricultural individuals (Figs 2 and 3).

Wing traits

Larval growth on drought-stressed plants was predicted to result in reduced forewing melanization, forewing aspect ratio and wing loading, particularly in agricultural females (predictions 1, 2 and 3). Males had significantly darker forewings than females (mean \pm SE females = 59.08 ± 0.45 , males = 52.70 ± 0.38 ; $F_{1,426} = 152.80$, $P << 0.001$). Furthermore, those males and females that developed for longer became significantly darker (slope parameter for covariate development time in GLMM = -0.72 , $F_{1,426} = 29.81$, $P << 0.001$). There were no significant differences across landscape types ($F_{1,2.35} = 1.35$, $P = 0.26$), nor between host plant treatment groups ($F_{1,426} = 0.15$, $P = 0.70$) in forewing melanization. There were no significant interaction effects.

Individuals that developed on drought-stressed plants had significantly lower forewing aspect ratios (mean \pm SE control plants = 1.76 ± 0.002 , drought-stressed plants = 1.74 ± 0.002 ; $F_{1,354} = 26.52$, $P << 0.001$). Variation between landscapes was smaller than between the populations within landscapes (fixed effect of landscape, $F_{1,2.01} = 0.32$, $P = 0.63$; random effect of population,

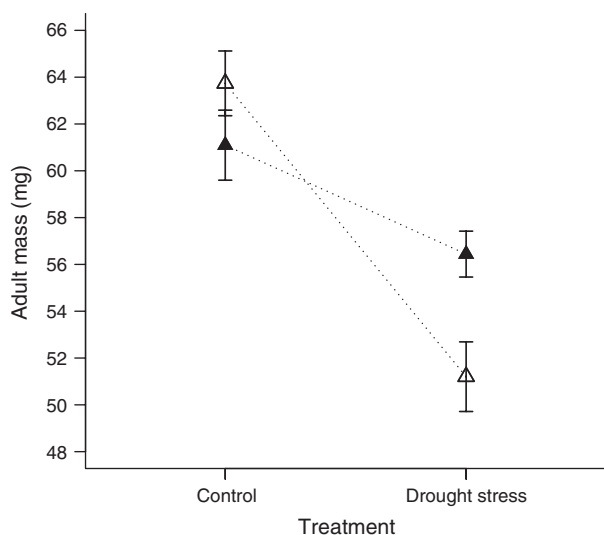


Figure 2 Mean adult mass at eclosion (\pm SE) for individuals from woodland (closed triangles, both populations pooled) and agricultural (open triangles, both populations pooled) landscapes reared on control and drought-stressed host plants.

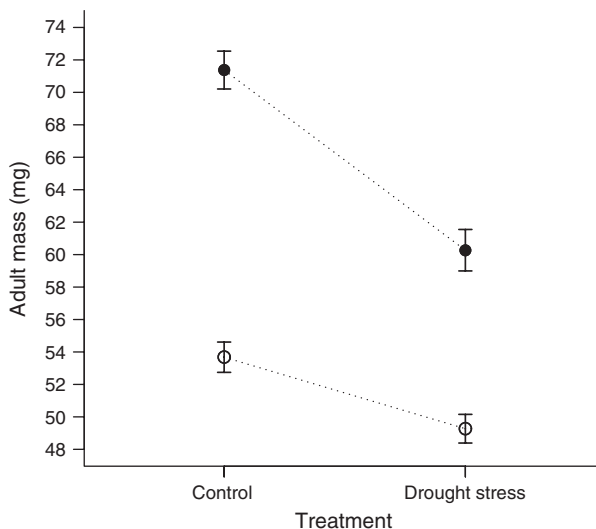


Figure 3 Mean adult mass at eclosion (\pm SE) for male (open circles) and female (closed circles) *P. aegeria* reared on control and drought-stressed host plants.

$F_{2,354} = 27.78$, $P << 0.001$, which accounted for 10.8% of the total variation). Females had significantly lower forewing aspect ratios than males (mean \pm SE females = 1.73 ± 0.002 , males = 1.76 ± 0.002 ; $F_{1,354} = 64.82$, $P << 0.001$). There were no significant interaction effects.

Individuals that developed for longer had a smaller wing loading (slope parameter for covariate development time in GLMM = -0.0019 , $F_{1,379} = 37.70$, $P << 0.001$). Variation between landscapes was smaller than between the populations within landscapes (fixed effect of landscape, $F_{1,2.05} = 0.29$, $P = 0.64$; random effect of population, $F_{2,379} = 10.61$, $P << 0.001$, which accounted for 3.1% of the total variation). Individuals that developed on drought-stressed plants had significantly lower wing loadings (mean \pm SE control plants = 0.09 ± 0.001 , drought-stressed plants = 0.08 ± 0.001 ; $F_{1,379} = 20.84$, $P << 0.001$). There was a significant difference between the sexes in wing loading ($F_{1,379} = 204.64$, $P << 0.001$), and there was a significant host plant treatment by sex interaction effect ($F_{1,379} = 11.95$, $P = 0.00061$). Across both host plant treatment groups, females had higher wing loading than males, development on drought-stressed plants significantly reduced wing loading in females, but not in males (Fig. 4).

Survival

Agricultural individuals reared on drought-stressed plants had a lower probability of survival than agricultural individuals reared on control plants (survival probability control, $75/85 = 0.88$; drought-stressed, $102/179 = 0.57$) and

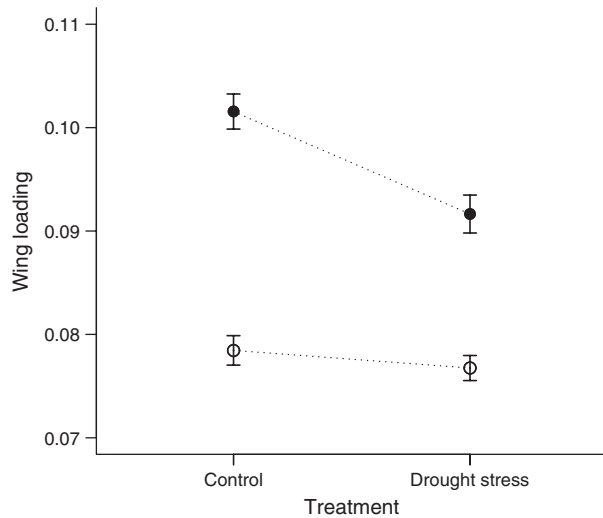


Figure 4 Mean wing loading (\pm SE) for male (open circles) and female (closed circles) *P. aegeria* reared on control and drought-stressed host plants.

woodland individuals (survival probability control, 82/93 = 0.88; drought-stressed, 195/211 = 0.92; survival time landscape effect coefficient = -0.0010 , $z = -0.013$, $P = 0.99$, plant treatment effect coefficient = -1.73 , $z = -4.70$, $P << 0.001$, landscape by plant treatment effect coefficient = 2.22 , $z = 4.02$, $P << 0.001$).

Reproductive output

Agricultural females were expected to have lower fecundity and reduced egg-hatching success. Of the 100 females tested in this experiment, four died before laying any eggs (one woodland control host plant-reared female, one woodland drought stress-reared female and two agricultural drought stress-reared females). These females were excluded from the lifetime fecundity and egg-hatching success analyses. Females that developed on drought-stressed plants had significantly lower lifetime fecundity (mean \pm SE control host plants = 133.58 ± 6.24 , drought-stressed host plants = 119.08 ± 6.92 ; $F_{1,88} = 7.28$, $P = 0.0083$). There was no significant difference in lifetime fecundity across landscape types ($F_{1,197} = 0.95$, $P = 0.43$). The covariates mean lifetime egg size and longevity both explained a significant proportion of the variation in lifetime fecundity; females that laid larger eggs laid fewer in total ($F_{1,88} = 40.30$, $P << 0.001$), and long-lived females laid more eggs ($F_{1,88} = 17.80$, $P << 0.001$). There were no significant differences between the populations in each landscape (random effect, $F_{2,88} = 1.56$, $P = 0.22$). The covariate adult body mass was nonsignificant and thus removed from the final model.

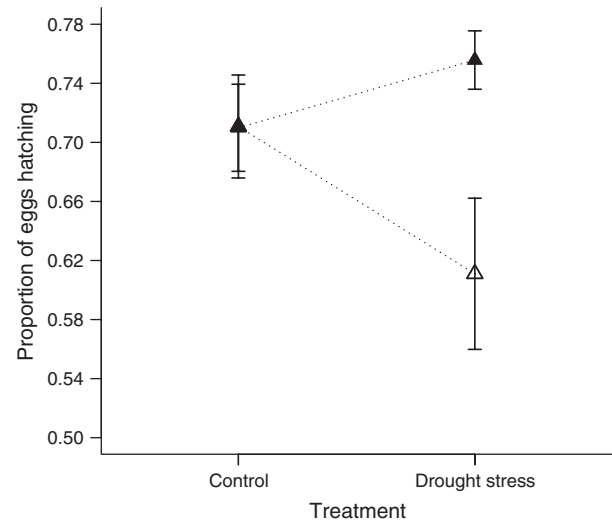


Figure 5 Mean hatching success of eggs laid by woodland (closed triangles, both populations pooled) and agricultural landscape (open triangles, both populations pooled) females reared on control and drought-stressed host plants.

The effect of drought stress on egg-hatching success was dependent on the landscape of origin (significant landscape by host plant treatment interaction effect, $F_{1,83} = 5.78$, $P = 0.018$; no main effect of landscape type, $F_{1,2} = 3.12$, $P = 0.22$ or plant treatment, $F_{1,83} = 1.12$, $P = 0.29$). For example, agricultural females that developed on drought-stressed plants laid eggs that had a significantly lower egg-hatching success (Table 1, Fig. 5). There were no significant differences amongst the populations in each landscape (random effect, $F_{2,83} = 1.63$, $P = 0.20$). The covariate egg size was nonsignificant and thus removed from the final model.

Discussion

The response of species to changes in water availability because of global climate change may be influenced by ecological and evolutionary mechanisms that operate locally at the level of individuals and populations and may result from a simultaneous interaction with other environmental variables such as anthropogenic land use (Schweiger et al. 2006). Our study focused on how male and female *P. aegeria* from landscapes that differ in their degree of anthropogenic land use (agricultural vs. woodland populations) were affected by development on drought-stressed host plants.

In line with our predictions, we observed that females were more adversely affected by development on drought-stressed plants than males. These sex-specific effects were, however, trait-specific and were related to changes in resource allocation to body mass, resulting in females

with significantly smaller adult body masses and lower wing loading. No sex-specific effects were observed for the traits development time, forewing melanization or forewing aspect ratio.

Compared with woodland individuals, when reared on drought-stressed plants, agricultural individuals had longer development times, reduced survival rates and smaller adult body masses. This suggests that when reared on *P. trivialis*, agricultural individuals need to grow for longer to obtain sufficient resources to reach the critical mass they require for pupation. It is possible that, in nature, female *P. aegeria* in agricultural landscapes actively select different host plants species and/or oviposition sites with different microclimates to minimize the impacts of reduced water availability on their offspring. However, additional studies would be necessary to explore this possibility further.

Across both landscape types, females that developed on drought-stressed plants had significantly lower lifetime fecundity. Given that adult body mass did not contribute to variation in female fecundity, these results indicate differences in fecundity between host plant treatment groups that are over and above those related to body mass *per se*. In addition, agricultural females that developed on drought-stressed plants laid eggs that had a significantly lower hatching success. Given that there were no differences in egg size across landscape types or host plant treatment groups, these results indicate egg provisioning differences between treatment groups that are over and above those related to egg size *per se*. This study therefore demonstrates that development on drought-stressed plants reduces fecundity, and has a landscape-specific effect on reproductive output in terms of reducing the quality or quantity of resources in eggs. It is known that in *P. aegeria* changes in egg provisioning negatively affect offspring development, both during the egg stage and then subsequently during the larval stage; particularly if larval growth occurs on low quality host plants (Gibbs et al. 2010a,b). As such, the results from the present study suggest that there is the potential for maternal growth on drought-stressed host plants to exert resource-related maternal effects that influence offspring performance in the next generation (cf. Gibbs and Van Dyck 2009).

Contrary to the findings of Talloen et al. (2004), in the present study growth on drought-stressed plants did not result in reduced forewing melanization. Further experiments are required to determine whether these differences observed across studies are because of context-dependent factors including (amongst others) population-specific differences in response to drought stress or across study differences in environmental conditions (e.g. temperature and humidity) and plant species used during larval development.

Across both landscape types, males and females that developed on drought-stressed host plants had significantly lower forewing aspect ratios, and females (but not males) also had a significantly lower wing loading. Hill et al. (1999) suggested that evolutionary changes in *P. aegeria* flight morphology may be related to colonization, because females of colonized sites in northern England had lower wing aspect ratios compared with females from continuously occupied sites. This suggests that male and female *P. aegeria* that develop on drought-stressed plants may have enhanced flight capacity during extensive flight, such as that required during dispersal to colonize new areas (but see Merckx and Van Dyck 2006). In Lepidoptera, however, a low wing loading is associated with higher levels of mobility (Dudley 2000). This suggests that female *P. aegeria* that developed on drought-stressed plants may actually have higher mobility than males, particularly during routine movements (i.e. the daily movement of individuals during foraging and oviposition; Van Dyck and Baguette 2005). A higher mobility would be beneficial for females as it would enable them to fly over wider areas searching for optimal host plants for their eggs (away from the natal drought-stressed host plant patch where they developed). Currently, the functional relationship between flight morphology and flight performance is not fully understood in butterflies, and further studies are therefore required to test how variation in *P. aegeria* flight morphology directly influences flight performance in nature.

Concluding remarks

The data from the present study provide a much-needed first step in elucidating the mechanisms by which low water availability may differentially influence woodland and agricultural population dynamics: (i) for agricultural individuals, larval development on drought-stressed plants reduces survival rates to adulthood and extends the time to adult maturation, both of which directly influence adult recruitment rates at the population level, (ii) adults that develop on drought-stressed plants have lower forewing aspect ratios that may enhance their dispersal capacity and colonizing potential, and thus may facilitate the movement of individuals out of drought-stricken areas and (iii) females that develop on drought-stressed plants have a lower reproductive output (i.e. reduced fecundity), and agricultural females are further disadvantaged by their decreased resource allocation to egg provisioning that reduces egg-hatching success. Overall, these data indicate that *P. aegeria* populations will be susceptible to an increase in the frequency of summer drought and demonstrate that agricultural populations will be particularly negatively affected by increased spatial heterogeneity

in precipitation levels predicted under current climate change scenarios.

It has been shown that the presence and distribution of woodland and woodland elements in the landscape matrix have an impact on dispersal and colonization in *P. aegeria* (Hill et al. 2001; Chardon et al. 2003). In periods of moderate drought stress, there may always be suitable host grasses for oviposition dotted around in cooler and wetter microclimates in woodlands or in taller hedgerows, but the searching efficiency of females will be an important determinant of whether females are actually able to find these sites. In this context, there is an intriguing difference in the perceptual range of *P. aegeria* from woodland landscape or from agricultural landscape populations. Merckx and Van Dyck (2007) showed that wild-caught males of an agricultural landscape population were better able to detect target habitat like a hedgerow or woodlot in an agricultural landscape matrix from a wider distance than were males of a woodland landscape population. This result was recently also confirmed for females that were reared in the laboratory from populations of the two landscape types (E. Öckinger and H. Van Dyck, unpublished data). Hence, based on these results, and the results of our study, functional connectivity may be different for individuals from populations across the two landscape types.

Our results suggest that climatic conditions interfere with expansion and dispersal patterns. The direct impact of weather conditions on adult activity has been long appreciated in these flying heliotherms (e.g. Heinrich 1986), but here we also show evidence of indirect effects through developmental processes. Contrary to assumptions in several ecological studies, dispersal is not a fixed species-specific life-history trait, and there is growing evidence for the importance of intraspecific- and between-population variation (Baguette and Van Dyck 2007; Stevens et al. 2010). The way functional morphology and life-history traits of organisms are shaped in rapidly changing anthropogenic environments is a growing eco-evo-devo field that will have much significance for eco-evolutionary conservation in the era of global change.

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Data archiving statement

Data for this study are available in the Environmental Information Data Centre (EIDC) at the NERC Centre for Ecology & Hydrology.

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