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Artificial light at night reduces larval survival and constrains female body mass in a capital breeding moth

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ABSTRACT

Light pollution, caused by artificial light at night (ALAN), affects an ever-increasing area of the Earth and evidence is piling up on its negative effects on organisms, including insects. Besides direct sensory and physiological effects on adult behaviour, ALAN may also affect larval growth and developmental life cycle regulation (e.g., diapause induction). Moth species whose larvae are mainly diurnal may also be sensitive to the disruption of the day-night cycle by ALAN, but species with such an ecological profile remained understudied so far. The garden tiger moth *Arctia caja* mainly shows diurnal activity at the larval stages and adults are capital breeders that do not feed at all. In a split-brood rearing experiment, caterpillars of the F_1 and F_2 generation from wild-caught females were individually grown under either ALAN or control-dark conditions. We tested for constraints of ALAN on larval survival and development, and the consequences for body mass. We showed evidence for increased larval mortality under ALAN conditions in both the F_1 and F_2 generation. ALAN caused accelerated larval development by disturbing the induction of a feeding arrest (i.e., larval diapause). Pupal mass was lower under ALAN conditions, but only so in females. Capital breeders like *A. caja* are expected to be particularly affected by a decrease in female body mass since this will negatively affect fecundity and adult lifespan. Therefore, our results suggest that long-term exposure of moth populations to ALAN negatively affects capital breeding performance and hence population performance.

Introduction

Light pollution, caused by artificial light at night (ALAN) has long been an underestimated stressor, or even threat, to nocturnal organisms and their ecological interactions (Longcore & Rich, 2004). In Europe, 99 % of surface area experiences some level of light pollution (Falchi et al., 2016) and the area and radiance of ALAN are still increasing (Kyba et al., 2017). Several mechanisms contribute to the direct effects ALAN has on organisms with a complex life cycle, such as holometabolic insects (Owens & Lewis, 2018). Firstly, light pollution may have direct sensory effects on adult behaviour. Many insects navigate using celestial bodies (Dacke et al., 2021; Sotthibandhu & Baker, 1979), but these marking points can become masked by skyglow (Falchi et al., 2016). During flight, moths and other nocturnal insects maintain correct body positioning by orienting their dorsal side towards the (celestial) light, but as a side effect, they are disturbed by showing a similar response to artificial light sources (Fabian et al., 2024). This can draw them away from favourable habitat (Owens et al., 2020). ALAN can reduce the visibility of essential feeding sources like flowers (Deora et al., 2021) and reduce response to mating signals (Owens & Lewis, 2018). Secondly, light pollution can have direct physiological effects on adult insect behaviour as it disturbs the biological clock through a perturbed natural day-night cycle. This may affect physiological pathways (e.g., melatonin production: Jones et al., 2015), but also reproductive behaviour (Botha et al., 2017; van Geffen et al., 2015) as well as feeding behaviour (Cieraad et al., 2022; van Langevelde et al., 2017).

However, the effects of ALAN are not likely to be limited to the behaviour of adult insects only. A few studies on moths have indeed shown effects on larval development; moths bred under light pollution regimes have shorter development times (Merckx et al., 2023; van Geffen et al., 2014) and lower body mass (Grenis & Murphy, 2019; van Geffen et al., 2014). There is also evidence for the disruption of diapause induction (Merckx et al., 2023; Schroer et al., 2019; van Geffen et al., 2014), which may, in turn, jeopardise winter survival. We are only starting to learn how ALAN could affect insects across the larval and pupal stages of their complex life cycle as those stages have different ecological relationships with the environment than adults.

For the regulation of the life cycle, insects rely on environmental

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information, for example, photoperiod, often together with temperature (Saunders, 2009). When ALAN extends the photophase into the night, the development and life cycle regulation of nocturnal juvenile stages can be affected (Durrant et al., 2018; Grenis & Murphy, 2019; Merckx et al., 2023; van Geffen et al., 2014). However, such effects could equally impact larvae which mainly have diurnal feeding activity. So far, developmental effects of ALAN on species with diurnal larvae have received only little, if any, attention.

In this study, we investigated potential constraints of ALAN on the survival, larval growth, life cycle regulation (i.e., feeding arrest or diapause induction) and body mass acquisition in the garden tiger moth *Arctia caja* L. (Lepidoptera: Erebidae). The adults are nocturnal, but the larvae are mainly diurnal. Moreover, *A. caja* has a capital breeding lifestyle, hence, larval feeding conditions have a direct impact on adult phenotype and performance as adults do not feed. Under ALAN, feeding time is predicted to increase (Haynes et al., 2023). Therefore, we expect this to lead to faster development and increased body mass, especially in females because of the relationship between body mass and fecundity (Heisswolf et al., 2009; Lamunyon, 1997). Our experimental test was conducted with both F_1 and F_2 generation caterpillars.

Materials and methods

Study species

The garden tiger moth *Arctia caja* is a widespread moth species in the temperate and subpolar zones of the Holarctic region (GBIF Backbone Taxonomy, 2024). In most of its distribution range, the species has one generation flying in the summer (from June to August in Belgium), but at the southern part of its range, it usually has a second generation (Bues & Poitout, 1984). Young caterpillars (i.e., larval stages L3 to L5) go through a feeding arrest in order to hibernate. In terms of both habitat and host plant use, *A. caja* is characterized as a generalist. Although the species is considered to be (rather) common throughout most of its range, there are nevertheless indications that it has declined significantly over the past few decades, at least in NW Europe including the U. K. where it is considered "vulnerable" (Conrad et al., 2002, 2006), and the Netherlands where it is considered "near threatened" (Ellis et al., 2013). In Flanders (North Belgium) where we sampled females, *A. caja* is currently in the "least concern" category (Veraghtert et al., 2023). Its decline is associated with climate change and habitat fragmentation (Conrad et al., 2002) and comes with changes in wing shape and a strong loss of genetic diversity (Anderson et al., 2008).

Female sampling and breeding conditions

Young larvae of wild-caught females of *Arctia caja* (i.e., F_1 generation) were submitted to a split-brood breeding experiment in a climate chamber in the lab with a control and an ALAN treatment. Next, the breeding experiment was repeated with F_2 generation larvae, which resulted from crossbreeding between males and females of the different families in the F_1 breeding experiment; inbreeding was not allowed. Females were captured with a Skinner light trap with mercury vapour lamp at the end of August 2021 in two sites in Hoegaarden, central Belgium. They were brought to the lab where they were kept individually in plastic boxes (18.5 × 18.5 × 20 cm) with fine mesh netting on top. Each box contained a *Plantago lanceolata* host plant for egg laying during two days. Eggs hatched after *c*. 10 days and young larvae were fed greenhouse-grown *P. lanceolata* until the start of the experiment.

During the experiment, larvae were reared in a climate chamber in individual rectangular plastic boxes with several 1-mm holes for aeration, a piece of paper towel, and in the F_1 experiment with a metal grid (1 × 1 mm) 1 cm above the bottom of the box. Diurnal light was provided by VEGELED LO250 floodlights (Colasse, 4000K; 80000 lux; Fig. S1, suppl. information). Every two days, the larvae were fed with fresh leaves of *P. lanceolata*. Until the fifth instar (i.e. when larvae lose the white dorsal line), greenhouse-grown host plants were used, while later instars were fed on wild-picked plants. At feeding, the larvae were checked for moulting. Relative humidity inside the boxes was increased with a plant mister. After replacing the leaves, the position of the boxes was randomized. The paper towels were replaced and faeces removed every three weeks for small larvae and every ten days for large larvae. Prior to pupation, the larvae spin a cocoon against a side of their box and after a few days they pupate. Pupae were removed from their cocoons seven days after pupation and weighed (Mettler MT5 microbalance; precision $\pm 10^{-5}$ g). They were then kept in the same box with a fresh piece of paper towel; the remaining plant material, cocoon and grid were removed. All adults were kept until their natural death, after which they were stored in the freezer (–21 °C). Dead adults were dried for at least 24 h at 60 °C in an oven (Jouan EB170) and their dry body mass was measured with the same microbalance.

F_1 generation

Offspring of wild-caught females ($N = 3$) were reared in a single climate chamber under a day-night cycle of LD 15:9 ($T_{day} = 21$ °C, $T_{night} = 16$ °C). Of each family, twenty-one larvae received ALAN from two LED lights placed at opposite sides of the ALAN treatment (Philips 1.4 W, 2700 K; 25.92–96.50 lux; measured in ten random rearing boxes per treatment with a Brannan Light Meter; Fig. S2, suppl. information). An equal number of larvae experienced control dark nights (0.40–0.63 lux). Rearing boxes were grouped per treatment and were located at opposite sides of the climate chamber and were switched sides after replacing the leaves (Fig. S3, suppl. information). The control treatment was shielded by polystyrene plates. Because the number of instars varied between individuals, we chose to distinguish eight larval stages based on size, colour and the amount of hair (Fig. S4, suppl. information). The date of transition between those stages was registered. Individuals reaching the pupal stage only after day 180 were considered to have gone through a feeding arrest (Fig. S5, suppl. information). To produce the F_2 generation, non-related F_1 males and females grown under the control treatment (i.e., experimental individual supplemented by spare individuals, grown in the same climate room under similar lighting conditions, to obtain maximal offspring numbers and diversity) were allowed to copulate in the same boxes the day after eclosion. After copulation, the female was transferred to a transparent plastic box with fresh paper towel for oviposition.

F_2 generation

In total, 14 F_2 families were established by crossing males and females from the offspring of the wild-caught females. From each family, fourteen larvae were kept in a climate chamber at a day-night cycle of LD 16:8 ($T_{day} = 23$ °C, $T_{night} = 18$ °C). Each brood was split over two treatments; half of the larvae were grown under control dark nights (0.10–0.20 lux) and the other half received ALAN from one LED light (Philips 1.4 W, 2700 K; 9.10–31.97 lux). The ALAN larvae were also the first generation to experience ALAN, as their parents were reared under control conditions. Location and shielding of the treatments were similar to the F_1 experiment (Fig. S6, suppl. information). When replacing the leaves, we registered whether a larva had eaten or not to calculate its feeding frequency (days larvae had eaten/duration larval period). All moults were counted and the corresponding dates were noted. Individuals that reached the pupal stage after day 250 were considered to have gone through a feeding arrest, but one individual with a larval development time of 264 days was moved to the non-feeding arrest category because our feeding data did not indicate any feeding arrest (Fig S5, suppl. information).

Statistical analysis

First, we tested for differences in survival between treatments using

generalized linear mixed models (GLMM) with a binomial error distribution. Differences in survival over time were tested using Kaplan-Meier estimation. Linear mixed models were used to test differences in pupal and adult dry body mass between sexes and treatment and their interaction effect. For the F_2 generation, the feeding frequency (proportion of days that larvae fed) was also included as a factor as well as the interaction effects with sex and treatment, respectively. Because of difference in the datasets, differences in the occurrence of a feeding arrest were tested with a χ^2 test for the F_1 generation, and with a GLMM with a binomial error distribution for the F_2 generation. Effects of sex, treatment (and feeding frequency for the F_2 generation) and their interaction effects on the duration of the larval, pupal and adult stage were tested using GLMMs with a Poisson error distribution. Family was included in all mixed models as a random factor. Interaction effects with $p > 0.1$ were removed from the models. Normality of model residuals was assessed visually with a QQ plot and by performing a Shapiro-Wilk normality test. Overdispersion was found for models with duration of the larval period, which was solved by adding an observation-level random factor to these models. All analyses were performed in R 4.3.0 (R Development Core Team, 2023). In the results section, we adopted the language of evidence (Muff et al., 2022). Raw means and SE's are reported in the suppl. information (Table S1-2), as well as sample sizes (Table S3). All data and R code used for the analyses are available on request from the corresponding author.

Results

Larval mortality

For the 126 larvae of the F_1 generation, we found very strong evidence for higher larval mortality under ALAN than under the control treatment (56/63 and 28/63, resp.) (Table 1). ALAN larvae died on average earlier in their development than did larvae in the control treatment (treatment: $\chi^2 = 63.68$, $p < 0.001$; Fig. 1), and they mainly did in the final larval stages, while under the control treatment, they mainly did so at the hibernating stages (Fig. S7, suppl. information). For the 224 larvae of the F_2 generation, we also found strong evidence for higher larval mortality under ALAN than under the control treatment (70/98 and 53/98, resp.) (Table 1). Mortality rate was especially higher between day 150 and 200 (treatment: $\chi^2 = 9.66$, $p = 0.002$; Fig. 1).

Development

In the F_1 generation all individuals in the control treatment showed a feeding arrest, while this was the case for only one female in the ALAN treatment (Table 1 and Fig. 2a). As a consequence, larval development was on average 51.8 % shorter under the ALAN treatment than under the control treatment (Table 1 and Fig 2b). There was also moderate evidence for sexual dimorphism in pupal development time, since males took 15.8 % more time to develop than females (Table 1 and Fig. 2c). In the F_2 generation, under the ALAN and control treatment, 11.1 and 80.0 % of the females, respectively, showed a feeding arrest, while in males this was 38.9 and 59.1 %, respectively (Table 1 and Fig. 2a). The larval stage lasted longer under ALAN than under the control treatment at a low feeding frequency, but shorter at high feeding frequency (Table 1 and Fig. 2b). Under the ALAN treatment, pupal development was 11.1 % shorter compared to the control treatment (Table 1 and Fig. 2c).

Body mass

For the F_1 generation, we found some evidence for an interaction effect between sex and treatment on pupal mass; ALAN females weighed 18.6 % less than control females, while ALAN males weighed 17.7 % more than control males (Table 1 and Fig. 2d). There was some evidence for higher dry body mass in females and weaker evidence for higher dry body mass under the ALAN treatment compared to the control treatment (Table 1 and Fig. 2f). In females of the F_2 generation, pupal mass was 8.8 % lower under the ALAN treatment than under the control treatment and it increased with feeding frequency. In contrast, male pupal mass did not vary with treatment nor feeding frequency (Table 1 and Fig. 2d and e). Overall, dry body mass decreased with feeding frequency and, in line with the known sex dimorphism, females were 63.1 % heavier than males (Table 1 and Fig. 2f).

Discussion

Our results provide evidence for negative effects of ALAN on larval survival, the occurrence of a feeding arrest and larval development time, and a related positive effect on feeding frequency in a moth with diurnal larvae and a capital breeding life style. ALAN effects on body mass were sex-dependent, with negative effects in females and none to positive effects in males.

We showed increased larval mortality under ALAN conditions. This is in contrast to a study on the nocturnal larvae of the noctuid moth

Table 1
Statistical output for differences in mortality and development in the F_1 and F_2 generation. All tests are based on d.f. = 1. Significant p-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

	F_1	χ^2	p	F_2	χ^2	p
Mortality	Treatment	23.34	**< 0.001**	Treatment	6.68	**0.010**
Occurrence of feeding arrest	Sex	0.68	0.408	Sex	0.20	0.655
	Treatment	28.65	**< 0.001**	Treatment	9.49	**0.002**
				Sex x Treatment	3.71	0.054°
Feeding frequency				Sex	0.33	0.563
				Treatment	3.54	0.060°
Duration of larval period	Sex	2.38	0.123	Sex	1.25	0.263
	Treatment	164.29	**< 0.001**	Treatment	8.41	**0.004**
				Feeding frequency	227.81	**< 0.001**
				Treatment x Feeding frequency	9.36	**0.002**
Duration of pupal period	Sex	4.10	**0.043**	Sex	0.21	0.650
	Treatment	0.010	0.922	Treatment	4.66	**0.031**
Pupal mass	Sex	3.46	0.063°	Sex	0.00	0.987
	Treatment	0.53	0.468	Treatment	5.55	**0.019**
	Sex x Treatment	3.87	**0.049**	Feeding frequency	4.73	**0.030**
				Sex x Treatment	3.26	0.071°
				Sex x Feeding frequency	3.37	0.066°
Dry body mass	Sex	4.06	**0.044**	Sex	31.73	**< 0.001**
	Treatment	3.73	0.053°	Treatment	0.00	1.00
				Feeding frequency	12.18	**< 0.001**

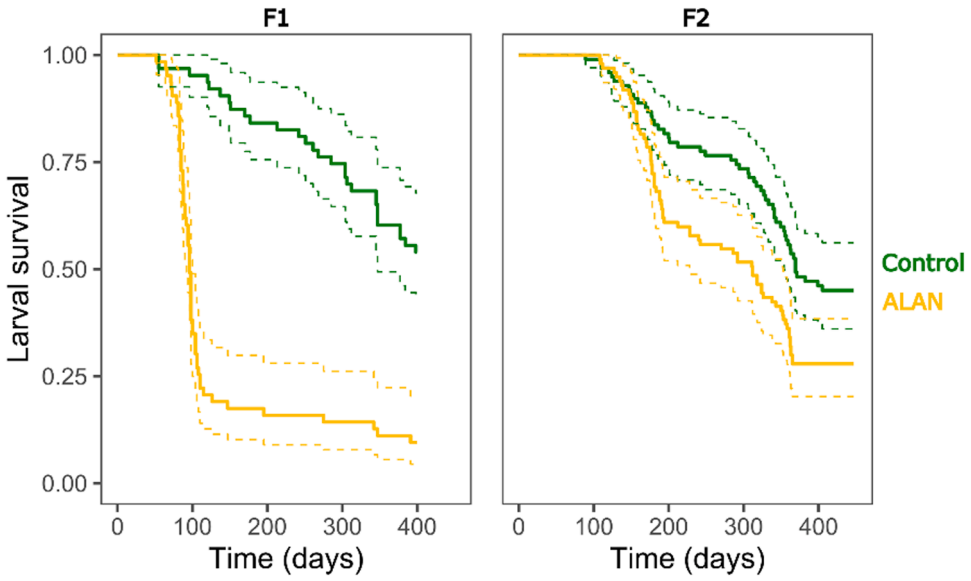

Fig. 1. Larval survival curves and 95 % confidence intervals (broken lines) under the control and ALAN treatment for the F_1 and F_2 generation.

Apamea sordens, which did not show an effect of light pollution on mortality (Grenis & Murphy, 2019). A couple of studies in different taxonomic groups have shown that ALAN can lead to an increase in stress levels (Ayalon et al., 2019; Grunst et al., 2020; McLay et al., 2018), defined as a deviation from homeostasis. When stress builds up, it could eventually lead to elevated mortality rates (McLay et al., 2017; Oconnor et al., 2019). However, we are not aware of such stress-related effects in moths. One mechanism by which ALAN could have affected the caterpillars of *A. caja* is through the disruption of sleep (Helfrich-Förster, 2018). If this causes damage (or lack of physiological recovery) to accumulate chronically throughout development, this may have led to the observed increased mortality, since our experiments excluded predation effects (Vaccaro et al., 2020), but this hypothesis remains to be tested. Chronic stress by light pollution can also work through a different mechanism, which would lead to a weakened immune system under ALAN conditions (Adamo, 2017; Bedrosian et al., 2011; Durrant et al., 2020). In the latter scenario, the effect of omnipresent pathogens may become stronger, leading in turn to higher mortality rates like we observed in the late instars under the ALAN treatment. Larval mortality under the ALAN treatment was more pronounced in the F_1 generation compared to the F_2 generation. The F_2 generation is composed of the direct offspring of the surviving individuals of the F_1 generation. Therefore, some selection may already have taken place during the F_1 generation experiment due to lower survival of some genotypes and individuals killed by pathogens (Kernbach et al., 2018), which could explain the observed decrease in larval mortality. However, our study was not designed for studying selection effects with a quantitative genetic approach, but such a study is now warranted.

Previous studies have shown diapause disruption by ALAN leading to faster development, at least under laboratory conditions (Merckx et al., 2023; Schroer et al., 2019; van Geffen et al., 2014). Here, we showed the same for caterpillars with a diurnal activity peak and larval hibernation. Diapause and its proper timing are essential for overcoming unfavourable conditions, mainly during winter. Outdoor breeding experiments are now warranted to test whether the significance of our results holds under natural conditions, with changing photoperiod and weather conditions. The reduced occurrence of feeding arrest observed in the control treatment for the F_2 generation could be expected given the high temperatures and long photoperiod. However, F_2 males in the ALAN treatment showed a higher incidence of feeding arrest than the F_1 males. Potentially, other factors are also at play here, including host plant quality (Friberg & Wiklund, 2010) and maternal effects like egg lipid content (Scharf et al., 2010), timing of egg deposition (Saunders, 1987) and maternal diapause history (Huestis & Marshall, 2006). Interestingly, based on a study by Bues and Poitout (1984), the photoperiod in our experiment should not have resulted in a feeding arrest. However, this study was conducted with moths from Southern France, where *A. caja* usually has two generations a year in contrast to one generation in our study area at a higher latitude, which can lead to differences in critical photoperiod for diapause induction. Furthermore, other factors like humidity and host plant quality can affect diapause induction alongside photoperiod and temperature (van Houten & Veenendaal, 1990).

We showed a lower pupal mass in females of the ALAN treatment compared to control females. In moths, female pupal mass is usually positively related to fecundity (e.g., Garrad et al., 2016; Heisswolf et al., 2009; Lamunyon, 1997). Therefore, if moth populations remain exposed to light pollution for longer periods, we could predict negative effects on population abundance, unless such losses would be compensated by immigration of females from nearby populations in non-light polluted areas. Our results strengthen the evidence for negative effects of ALAN on moth body mass (Grenis & Murphy, 2019; van Geffen et al., 2014). Capital breeders like *A. caja* can be expected to be intrinsically more affected since, unlike income breeders, they do not feed as adults and thus cannot make up for any nutrient deficiencies built up during the larval stages. On the other hand, ALAN can distract income breeders from adult feeding behaviour (Cieraad et al., 2022; van Langevelde et al., 2017), which could compromise egg production and thus fitness. Our study contributes to our knowledge about ALAN-related effects in insects with a particular eco-evolutionary profile (i.e. diurnal larval feeders with capital breeding adults), which is helpful for broadening our understanding of this widespread global change issue.

Our results showed evidence for sex-dependent differences in body mass acquisition under ALAN. Males in the ALAN treatment had a similar or higher pupal mass than control males. This is opposite to the results of a study on the noctuid *Mamestra brassicae* (van Geffen et al., 2014), which only showed negative effects on male pupal mass, but not for females. However, stressors may have stronger negative effects on females than on males in species with female-biased size dimorphism (Teder & Kaasik, 2023) as they will need more energy for full development. This may be particularly the case for capital breeding species.

In the F_1 generation, we found opposite results for dry body mass compared to pupal mass. Dry body mass was higher for both sexes under the ALAN treatment than under the control treatment. However, we have to keep in mind that nearly all individuals of the control treatment

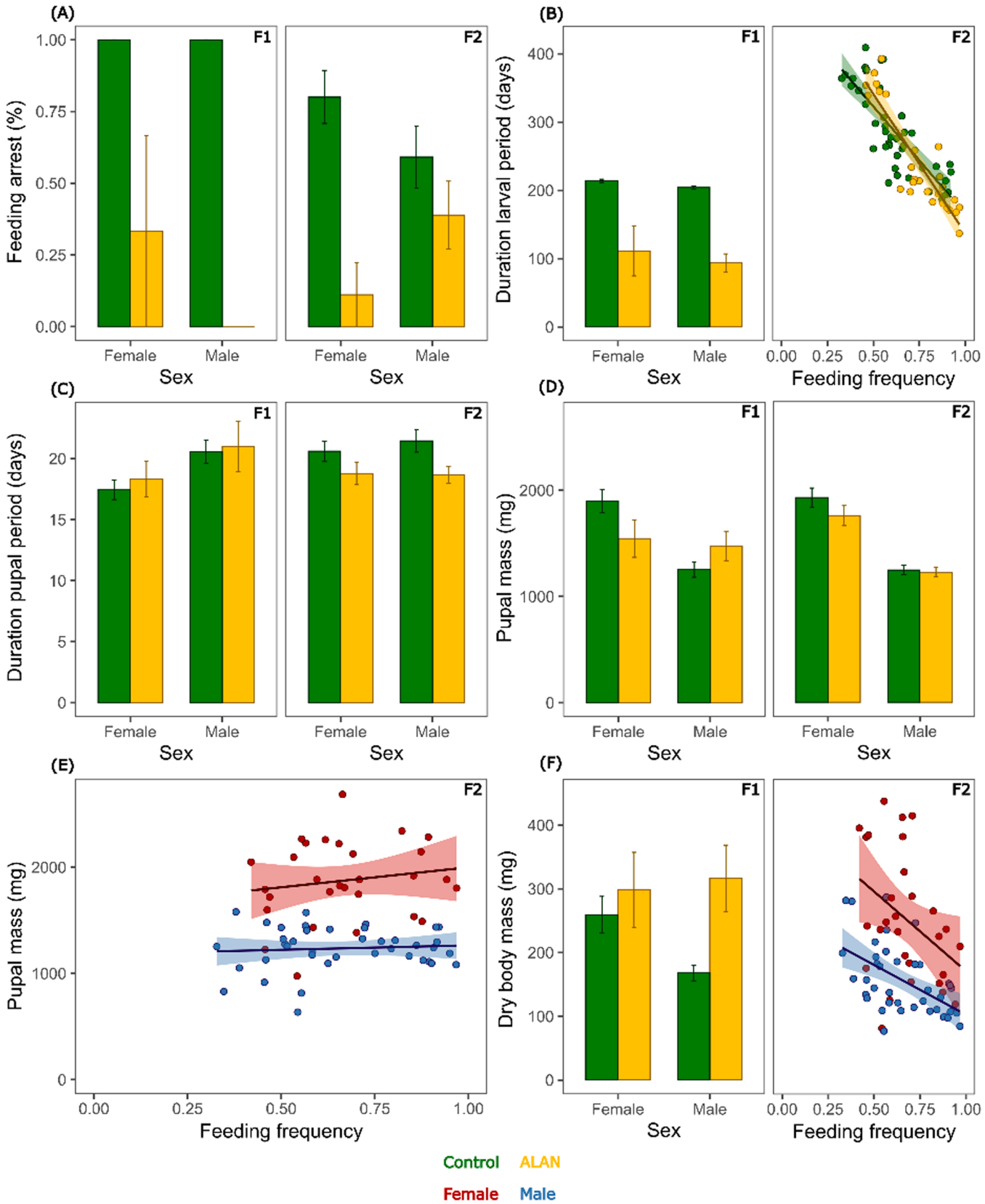

Fig. 2. (A-D,F) Raw mean values ± SE feeding arrest, duration of the larval and pupal stage, pupal mass and dry body mass in F_1 and F_2 generation female and male Arctia caja under the control and ALAN treatment. (B) Raw values and linear regression lines (and 95 % confidence intervals: shaded area) of duration of the larval stage in function of feeding frequency under the control and ALAN treatment. (E-F) Raw values and linear regression lines (and 95 % confidence intervals: shaded area) of pupal mass and dry body mass as a function of feeding frequency in females and males.

were allowed to copulate and these females produced eggs till the end of their lifetime, while only one male and female of the ALAN treatment did so. This could have led to strong weight losses in the control adults, especially since it is a capital breeding species, and may therefore explain, at least partly, this difference in pupal and adult dry mass.

In many ALAN studies, control conditions are set to full darkness . However, nights are never completely dark, certainly not in our study area (i.e., Flanders) (Falchi et al., 2016). Therefore, we chose to work with a light intensity for our control treatment that is comparable to skyglow (*cf.* Merckx et al., 2023) and an ALAN treatment that is *c.* two orders of magnitude stronger in intensity. Despite the higher light intensity for the control treatment, we still found clear differences in terms of impact on larval development compared to the ALAN treatment. However, it would be interesting to investigate whether our control treatment also has a different impact compared to lower light intensities (i.e., below 0.05 lux), as this would suggest effects of skyglow on larval development (Merckx et al., 2023).

Our study focused on what happens to a caterpillar when it grows up under ALAN. Studies on the ermine moth *Yponomeuta cagnagella* have found reduced flight-to-light response in urban, light-polluted populations (Altermatt & Ebert, 2016) and related changes in wing morphology (Van de Schoot et al., 2024), showing potential for evolution in moths to cope with living in light-polluted areas (but see Cieraad et al., 2022). It would therefore be interesting to explore potential evolutionary adaptation for development under ALAN in light-polluted populations, and whether development under ALAN can lead to changes in flight-related morphology. Whether the observed strong losses of genetic diversity in the garden tiger moth (Anderson et al., 2008) could have any significance for such evolutionary responses is currently not known.

Evidence for significant effects of ALAN on larval development in moths is compiling and, to that end, our study contributes to this by providing evidence of increased mortality, accelerated development and reduced body mass in females under ALAN. Potential consequences for individual fitness and population performance require more attention in future studies.

CRediT authorship contribution statement

Evert Van de Schoot: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Renate A. Wesselingh:** Writing – review & editing, Validation, Supervision, Formal analysis, Conceptualization. **Hans Van Dyck:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2025.03.008.

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