Larval development under continuous and dynamic light pollution alters sexual dimorphism in a moth species

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Abstract

1. Larval development under artificial light at night (ALAN) can affect adult body mass, often in a sex-specific way. However, it is still unclear whether ALAN also affects other morphological traits.

2. In this experimental study, we tested for differences in flight and fecundity-related morphology and wing melanisation in the noctuid moth *Agrotis exclamationis*, originating from populations under contrasting skyglow levels, and whose offspring was reared under either a dynamic ALAN, continuous ALAN or control dark treatment.

3. In response to ALAN, adult body mass and wing size were affected in a sex-specific way, resulting in altered sexual size dimorphism. Wing aspect ratio was lower in populations originating from higher skyglow levels, but only in males. Under ALAN conditions, relatively more mass was allocated to the abdomen and less to the thorax.

4. Sexual colour dimorphism was stronger in populations originating from higher skyglow levels as males from these populations had lighter coloured wings and females had darker wings compared to populations from lower skyglow levels.

5. We provide evidence for alterations of sexual dimorphism under ALAN. Different developmental effects of ALAN on males and females are likely to contribute to the significant though complex impacts of this type of sensory pollution in a wider range of moth and other insect species.

KEYWORDS

Artificial light at night (ALAN), dynamic lighting, Lepidoptera, mass allocation, sexual dimorphism, wing morphology

INTRODUCTION

Evidence is mounting for the impact of light pollution, caused by artificial light at night (ALAN), on insects (Owens & Lewis, 2018; Desouhant *et al.*, 2019; Owens *et al.*, 2020). Insects experience the impact of ALAN directly on adult behaviour as well as during larval development. Moreover, effects on larvae may have consequences for phenotypic trait expression at the adult stage. Both diurnal and nocturnal insects maintain proper body orientation during flight by keeping their dorsal body side up towards the distant natural celestial light sources. However, insects respond similarly towards nearby artificial light sources, leading to erratic flights and a typical flight-to-light response, both within (Fabian *et al.*, 2024) and beyond the area directly illuminated by ALAN (Degen *et al.*, 2024). However, not all insect species are attracted by ALAN; some are actually repelled by artificial light (Farnworth *et al.*, 2018). Some nocturnal insects have been shown to navigate using a stellar compass (Dacke *et al.*, 2021; Dreyer *et al.*, 2025), but skyglow, caused by the reflection and scatter of ALAN by the atmosphere and clouds, can mask celestial bodies (Falchi *et al.*, 2016) and therefore interferes with nocturnal insect navigation (Dreyer *et al.*, 2025). ALAN can affect larval development in several ways. For example, development under ALAN can alter growth rate (Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025a) and therefore also body mass (van Geffen *et al.*, 2014; Durrant *et al.*, 2018; Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025b, 2025a).

Sexual dimorphism is a widespread phenomenon in animals, including insects (Shine, 1989; Zhu et al. 2025). One of the best-studied examples is sexual size dimorphism (e.g., Esperk *et al.*, 2007; Teder *et al.*, 2021). In insects, sexual size dimorphism is usually female-biased (although there are exceptions: R ohner *et al.*, 2018), which is often associated with longer development time (Esperk *et al.*, 2007; Teder, 2014; Teder *et al.*, 2021) or increased growth rate in females compared to males (Knapp, 2014; Sõber *et al.*, 2019). More subtle differences may stem from differences in weight loss during adult eclosion (M olleman *et al.*, 2011; Van de Schoot *et al.*, 2025a). However, sex-specific responses to environmental conditions can alter trait values in females and males and can impact degrees of sexual dimorphism (Teder & Tammaru, 2005; Stillwell & Fox, 2007). There is evidence that ALAN can change the differences in body mass between the two sexes, albeit in varying directions (van Geffen *et al.*, 2014; Van de Schoot *et al.*, 2025b, 2025a). Whether these alterations extend to other size-related morphological traits is currently unknown. Yet relative mass allocation to thorax muscles and wing morphology play an important role for flight performance (Berwaerts *et al.*, 2002; Flockhart *et al.*, 2017). For example, Van de Schoot *et al.* (2024) showed that urban ermine moths (*Yponomeuta cagnagella*) had smaller wings than rural moths and that these differences related to the observed weaker flight-to-light response (Altermatt & Ebert, 2016), providing evidence for evolutionary changes in flight-related morphology driven by ALAN or other processes linked to urbanisation (e.g., habitat fragmentation, urban heat island and altered predation risk).

In Lepidoptera, sexual dimorphism is not limited to size: it can also concern wing colour, from completely different colour patterns to more subtle differences, for example, in pigmentation levels (Allen *et al.*, 2011). An example of the latter can be found in *Agrotis* moth species, in which females have darker wings than males (i.e., higher degree of melanisation). In insects, melanisation is associated with multiple functions, including thermoregulation (e.g., Goulson, 1994; Hegna *et al.*, 2013; Laakso *et al.*, 2021), desiccation resistance (Parkash *et al.*, 2009; King & Sinclair, 2015; Bai *et al.*, 2022), UV resistance (Ortonne, 2002; Debecker *et al.*, 2015) and immune response (Dubovskiy *et al.*, 2013; Srygley & Jaronski, 2022), amongst others. Melanin production can be matched to background

colours and patterns to increase camouflage against visual predators (Cook *et al.*, 2012; Edelaar *et al.*, 2017; Stavenga *et al.*, 2020). For example, at the end of the night, moths select substrates to spend the day on; background matching to avoid predation by visual predators is assumed to be a significant selection pressure on cryptic wing colour (e.g., Kang *et al.*, 2015). However, by illuminating the environment, ALAN can disturb proper background selection and efficiency, especially putting lighter-coloured species or individuals at a disadvantage (Briolat *et al.*, 2021; Bullough *et al.*, 2023). Moreover, larval development on drought-stressed hostplants (Talloen *et al.*, 2004) or under conditions of limited nutrient availability (Ethier *et al.*, 2015) can contribute to reduced melanin production. It has been shown that ALAN can cause physiological stress in different animal groups (Ayalon *et al.*, 2019; Grunst *et al.*, 2020; Petrović *et al.*, 2025), including insects (McLay *et al.*, 2018), which could also result into lower melanisation.

High skyglow levels indicate areas with high densities of artificial light sources. In such areas, insects are more likely to be attracted to an artificial light source and may experience its negative effects, such as lower mating success (van Geffen *et al.*, 2015; Owens & Lewis, 2022), disturbed feeding behaviour (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022) and increased predation risk (Wakefield *et al.*, 2015; Willmott *et al.*, 2019). Over the past decade, there has been an increasing search for new street lighting technologies that can reduce the negative impact of attraction or repulsion by ALAN in insects, but also in other nocturnal animals like bats (Lacoeuilhe *et al.*, 2014; Challéat *et al.*, 2021). For example, the transition to light-emitting diode (LED) streetlights allows for higher flexibility in regulating ALAN intensity, leading to the creation of dynamic ALAN. In such applications, streetlights are partially or fully dimmed at times of low or no traffic (Haans & de Kort, 2012). One example of dynamic ALAN are streetlights with motion detection that only switch on when traffic passes and switch back off after a short period of time, reducing ALAN exposure time and financial costs. Bolliger *et al.* (2020) showed that insect abundance was indeed lower near dynamic ALAN than continuously bright ALAN. However, its impact is not necessarily positive, as shown for aphids (Heinen *et al.*, 2023). Moreover, exposure to short ALAN pulses can already lead to erratic flight behaviour in adult moths (Fabusova *et al.*, 2024).

Most ALAN-studies on insects work with continuous light pollution, but as we also need to understand effects of more frequently applied dynamic light pollution, we used both types of ALAN in our current study.

In our study, we investigated in moths whether larval exposure to continuous and dynamic ALAN differently affects flight-related morphology and wing melanisation, and whether the observed responses differ between males and females. This allowed us to test the impact of ALAN on sexual dimorphism in adult traits. We used larvae of the noctuid moth *Agrotis exclamationis* originating from populations under either low-medium or high-medium skyglow levels, allowing us to also test for differential responses against the negative impact of flight-to-light behaviour under high-medium skyglow levels. A recent study on *A. exclamationis* showed that larval development under ALAN resulted in increased body mass (Van de Schoot *et al.*, 2025a). If this added mass was allocated to the flight muscles in the thorax or wings, it could be associated with increased flight performance (Berwaerts *et al.*, 2002; Flockhart *et al.*, 2017), and consequently with an increase in their flight-to-light response (Van de Schoot *et al.*, 2024). However, if mass gain is mainly allocated to the abdomen, then overall mobility could be reduced (Tigreros & Davidowitz, 2019), possibly with an increase in fecundity (Lamunyon, 1997; Heisswolf *et al.*, 2009) or longevity (Taylor *et al.*, 1998; Garrad *et al.*, 2016). The study of Keinath *et al.* (2021) showed that forewing length in *A. exclamationis* did not change over time with increasing light pollution, but they did not test for any other flight-related morphological traits. Previous studies that compared the effects of larval development under ALAN on male and female morphology, showed evidence of both increased sexual dimorphism due to lower body mass in males (van Geffen *et al.*, 2014) and reduced sexual dimorphism due to lower body mass in females (Van de Schoot *et al.*, 2025b). Previous work by Van de Schoot *et al.* (2025a) on *A. exclamationis* showed a tendency for stronger sexual dimorphism after development under dynamic ALAN, while it decreased under continuous ALAN; however, the interaction between ALAN treatment and sex was not significant. If high-medium skyglow levels would select for an adaptive response against mobility, which could lead to reduced flight-to-light (Van de Schoot *et al.*, 2024), and if we assume that a

mobility-fecundity trade-off occurs, we predict higher mass allocation to the abdomen and, consequently, lower investment in the thorax and the wings compared to moths living under low-medium skyglow conditions. We tested these hypotheses with a laboratory experiment.

METHODS

Study species and female sampling

The heart and dart *Agrotis exclamationis* L. (Lepidoptera: Noctuidae) is a common moth species that is widely distributed in the temperate and Mediterranean zones of the Palearctic region (GBIF Backbone Taxonomy, 2023). It is present in different kinds of open habitats including gardens and arable fields where the larvae can form a pest on a wide variety of crops (Baranek *et al.*, 2023). Adults have a relatively high dispersal capacity as they can fly several kilometres per night in tethered flight experiments (Jones *et al.*, 2016). However, in a mark-release-recapture study, Slade *et al.* (2013) showed a predicted and mean distance over 7 days of 277 m and 545 m, respectively. Like several other *Agrotis* species, females usually have darker wings than males (Waring *et al.*, 2015). However, both the proximate and ultimate factors explaining the sexual wing colour dimorphism are poorly understood.

For this study, the same specimens were used as in the study by Van de Schoot *et al.* (2025a). Gravid females were sampled in gardens under either low-medium skyglow levels (Southern Belgium: Sky Quality Meter (SQM) = 20.82–21.30 mag./arc sec²) or high-medium skyglow levels (Central Belgium: SQM = 19.50–20.43 mag./arc sec²) (data from http://www.lightpollutionmap.info; Figure S1, Supporting information). They were captured using both Skinner type light traps with a mercury vapour lamp and LedTraps with a 5050 UV LED strip (van Deijk *et al.*, 2024). Captured females were transferred to the lab for oviposition in transparent, plastic boxes (115 x 115 x 60 mm, Biopack) with 1-mm holes for aeration, paper towel and a 1.5-mL tube of 10 % honey-water solution. From the low-medium and

high-medium skyglow region, twelve females in seven gardens and eleven females in six gardens were sampled, respectively. Family groups of eggs and young larvae were kept in climate chambers in the same type of boxes under a day-night cycle of LD 16:8 (day temperature = 23 °C, night temperature = 18 °C). Until the start of the experiment, larvae were fed a mixture of wild-picked *Taraxacum officinale* and *Plantago lanceolata*.

Split-brood breeding experiment

Six to twelve second-instar larvae per family were transferred to a single plastic box per individual with aeration holes and a piece of paper towel (dimensions plastic box: 115 x 115 x 60 mm). They were equally divided over three treatment groups: (i) continuous ALAN from a single LED light (Philips 1.4 W, 2700 K; 9.10–46.7 lx) during the whole night; (ii) dynamic ALAN from a single LED light with one-minute pulses of light and variable time of darkness mimicking dynamic streetlights with movement detection (on: 10.3–44.2 lx, off: 0.16–0.23; time scheme in Table S1, Supporting information); (iii) control treatment with dark nights (0.03–0.16 lx). All treatments were replicated in two climate rooms under a day-night cycle of LD 16:8 (day temperature = 23 °C, night temperature = 18 °C). Larvae were fed ad libitum with pieces of wild-picked *P. lanceolata* leaves. Resulting adults were provided with a 1.5 mL tube of honey-water solution. Five days after eclosion, they were transferred to a freezer (–21 °C) for storage.

Flight-related morphology

<u>Thorax and abdomen mass</u>

Moth specimens were dried in an incubator for 4 h at 60 °C until stable dry body mass. Total dry body mass (m_{tot}) was measured using a microbalance (Mettler MT5 microbalance; precision ± 10^{-2} mg). Head,

thorax, abdomen and wings were carefully separated with a needle. Next, thorax and abdomen mass were weighed on the same balance. We also calculated relative investment in thorax and abdomen by dividing body mass by thorax and abdomen mass, respectively.

Wing morphology and melanisation

Scanned images were made of the dorsal surface of the right forewing (Epson Perfection V500 Photo Scanner). In case of significant damage to the right forewing, the left forewing was used instead. Forewing length (FWL), width (FWW) and area (FWA) were measured using ImageJ software (https://imagej.net/ij/index.html); marking points are shown in Figure S2 (Supporting information). Aspect ratio was calculated as $4 \cdot FWL^2/FWW$ and wing loading as m_{tot}/FWA (Berwaerts *et al.*, 2002; Van Dyck & Wiklund, 2002). Forewing melanisation was measured as the mean grey value in a predefined area at the centre of the wing between the oval and kidney mark (Vandewoestijne & Van Dyck, 2011) (Figure S2, Supporting information).

Statistical analysis

Effects of ALAN treatment, skyglow origin and sex as well as their two-way interactions, were analysed relative to flight-related morphology and wing melanisation using linear mixed models. Total body mass was included as a covariate in the models for forewing length, width, area and aspect ratio. Climate room was included as a covariate and sampling site and family were included as random variables in all models. When a significant treatment effect was found, the different ALAN treatments were compared using a post-hoc test with Benjamini-Hochberg correction. All analyses were performed in R 4.4.2 (R Development Core Team, 2022). In the results section, we adopted the language of evidence, which allows for a more nuanced approach to communicate scientific findings in line with the guidelines of Muff *et al.* (2022).

RESULTS

Table 1 summarizes the statistical output. Female body mass was greater under continuous and dynamic ALAN compared to the control treatment (continuous ALAN–control: $t_{130} = 2.73$, $p = 0.011$; dynamic ALAN–control: $t_{129} = 2.92$, $p = 0.011$); female body mass did not differ between the two ALAN treatments. The pattern was different in males. Although male body mass was significantly greater under continuous ALAN, as in females, it was not greater under dynamic ALAN (continuous ALAN–dynamic ALAN: $t_{128} = 3.47$, $p = 0.001$; continuous ALAN–control: $t_{127} = 4.00$, $p < 0.001$; Figure 1a). Hence, there is an interaction effect between the factors ALAN treatment and sex.

There was very strong evidence for higher relative thorax mass in males compared to females, and *vice versa* for relative abdomen mass (Figure 1b-c). Independent of sex, relative thorax mass was lower under continuous and dynamic ALAN than under the control treatment (continuous ALAN–control: $t_{132} = -4.19$, $p < 0.001$; dynamic ALAN–control: $t_{127} = -2.86$, $p = 0.014$), while the opposite was true for relative abdomen mass (continuous ALAN–control: $t_{133} = 5.35$, $p < 0.001$; dynamic ALAN–control: $t_{128} = 3.99$, $p < 0.001$; Figure 1b-c).

Interestingly, the body-mass corrected ALAN effects on forewing area were opposite in males and females. Female relative wing area tended to increase under ALAN, whereas it tended to decrease in males (Figure 2a). However, this was not the case for forewing length and width, since only the main effects of sex and of skyglow level at the population of origin were significant. Male wings tended to be longer and wider than in females (Figure 2b,d), and there was some evidence for longer forewings in moths originating from low-medium skyglow compared to high-medium skyglow populations (Figure 2c). Forewing aspect ratio was higher in males than in females when originating from low-medium skyglow populations, while the opposite relationship was found for moths originating from high-medium skyglow populations (Figure 2e). Females clearly had higher wing loadings than males (Figure 2f).

Sexual wing dimorphism in dorsal wing melanisation (i.e., females have darker wings than males) was more pronounced in individuals that originated from high-medium skyglow populations compared to the ones from low-medium skyglow populations (Figure 3).

DISCUSSION

Two previous studies have investigated the impact of light pollution on *A. exclamationis*. Keinath *et al.* (2021) showed that adult body size, but not relative wing length increased over a 137-year period with increasing light pollution. However, they found no direct correlation between light radiation levels and morphology, leaving open the possibility that other environmental factors that changed during this period are the main cause of increased body size (e.g., habitat fragmentation: Warzecha *et al.*, 2016; Merckx *et al.*, 2018). Van de Schoot *et al.* (2025a) investigated the impact of continuous and dynamic ALAN on larval development. They showed faster development, higher growth rate and increased adult body mass at eclosion under both types of ALAN. Our study makes a significant contribution by experimentally testing whether larval development under continuous and dynamic ALAN conditions affects sexual dimorphism in flight morphology and wing melanisation in adults of *A. exclamationis*. We also tested whether moths whose mother originated from high-medium skyglow populations responded differently compared to those from low-medium skyglow populations. In general, development under ALAN led to higher dry body mass. However, sexual dimorphism decreased under continuous ALAN, while it increased under dynamic ALAN. Gained body mass was mainly allocated to the abdomen. ALAN increased wing size in females, but resulted in smaller wings in males; this way reducing sexual size dimorphism. Moths originating from high-medium skyglow populations showed increased sexual dimorphism in wing melanisation. We discuss the potential mechanisms behind our results as well as the possible consequences for flight, fecundity and wing colouration under light pollution.

Variation in sexual dimorphism is often a result of sexual differences in phenotypic plasticity as a response to environmental conditions (Stillwell *et al.*, 2010). Interestingly, we show that male body mass increased more under continuous ALAN compared to females, thereby reducing sexual dimorphism. However, body mass in males did not increase under dynamic ALAN, while it did in females, thus increasing sexual dimorphism. Here, the sexual dimorphism of body size could not be explained by differences in larval development time or growth rate, but rather by the 25 % higher mass loss at eclosion in males compared to females (pupal mass tended to be higher in males than in females, Van de Schoot *et al.*, 2025a). Probably, females retain more water for egg production, while the higher water loss in males may facilitate flight performance (Molleman *et al.*, 2011). The lower mass gain in males compared to females under dynamic ALAN was already established in the pupal stage, and therefore probably stems from a different response during larval development. However, the mechanism behind this difference is still unclear as neither larval development time nor growth rate differed between sexes under dynamic ALAN (Van de Schoot *et al.*, 2025a). Moreover, studies on larval behaviour under different light conditions and on moth ecology in general are still very scarce.

In areas with high light pollution levels, lower overall flight performance could be beneficial for a moth because of reduced flight-to-light response (Van de Schoot *et al.*, 2024). ALAN had a positive effect on relative female wing area, but a negative effect on relative male wing area, leading to a loss of sexual dimorphism in this trait. Interestingly, this suggests that larval development under ALAN can lead to a reduced flight performance (Berwaerts *et al.*, 2002), and thus potentially flight-to-light response (Van de Schoot *et al.*, 2024), in males. Moreover, forewing aspect ratio is lower in males originating from high-medium skyglow populations compared to males from low-medium skyglow populations, while no difference was observed in females. This indicates that males from areas with stronger light pollution have lower flight performance (Berwaerts *et al.*, 2002). Male moths are usually more attracted to ALAN than females (Altermatt *et al.*, 2009; Garris & Snyder, 2010, but see Degen *et al.*, 2016), and this could potentially result in stronger selection against flight-to-light through reduced flight performance in males.

Alterations in body mass allocation can change the balance between fecundity and flight performance (Tigreros & Davidowitz, 2019). Both continuous and dynamic ALAN led to a higher relative mass allocation to the abdomen and a lower allocation to the thorax. These results suggest that the gained body mass is mainly used to increase fecundity (Lamunyon, 1997; Heisswolf *et al.*, 2009) at the expense of flight performance in both sexes (Berwaerts *et al.*, 2002). The latter may be compensated in females by the increased relative wing area, but in males, this is an additional indication of reduced flight performance after development under ALAN conditions. The accelerated larval development, higher body mass and increased allocation to fecundity could offset the negative effects of flight-to-light if the latter does not increase at the same time, which, at least for males, seems to be the case. So in terms of development, *A. exclamationis* does not seem to be negatively impacted by ALAN, unlike other species that do lose body mass (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025b).

As expected, we found the known sexual colour dimorphism in *A. exclamationis* with females being darker than males. The mechanism behind this dimorphism has not yet been revealed, but the insect-specific *yellow* gene family has been shown to be involved in melanin production (Li & Christensen, 2011; Miyazaki *et al.*, 2014). These type of genes also play important roles in eggshell formation, hardening and pigmentation (Claycomb *et al.*, 2004; Noh *et al.*, 2021), which potentially explains the higher melanisation levels in females, but this requires further research. Body colouration in insects can be under selection by human-induced rapid environmental changes. For example, climate warming usually favours lighter-coloured insects (Zeuss *et al.*, 2014; Valverde & Schielzeth, 2015; Clusella-Trullas & Nielsen, 2020; Haque *et al.*, 2024). For moth species that stay close to the ground, we could expect selection against lighter-coloured individuals to avoid higher visibility for predators under direct ALAN (Briolat *et al.*, 2021; Bullough *et al.*, 2023). Possibly the reverse is true for species that fly higher and thus would be more likely to be attacked from below as lighter individuals might be less conspicuous against a bright sky due to skyglow (Creemers *et al.*, 2025). Interestingly, in moths originating from high-medium skyglow populations, we showed an increase in colour dimorphism compared to low-

medium skyglow populations. Females from high-medium skyglow populations were darker, but in contrast, males were lighter. Although urbanisation levels are not significantly different at our sampling sites, we could not control for other environmental differences that can drive wing colouration. For example, mean temperatures in the high-medium skyglow region are higher, which can potentially explain the lower wing melanisation in males (Zeuss *et al.*, 2014; Valverde & Schielzeth, 2015); but differences in altitude (Parkash *et al.*, 2008) and chemical pollution (Skaldina *et al.*, 2018) may also play a role here.

Our results indicate reduced flight performance, especially in males, potentially lowering flight-to-light response (Van de Schoot *et al.*, 2024). Flight-to-light tests similar to the study by Altermatt *et al.* (2009) are now required to determine whether the propensity to be attracted to an artificial light source is indeed related to morphology in *A. exclamationis*. Likewise, it would be useful to investigate whether the increase in relative abdomen mass effectively results in higher fecundity and to what extent (Leather, 1988). The impact of skyglow level at the population of origin was limited, including a couple of interactions with sex. However, it should be noted that in our study area (Belgium), it was impossible to select sampling sites with zero or low skyglow (Falchi *et al.*, 2016), which would be interesting for future research.

Our paper contributes to the growing field of effects on sexual dimorphism in life history traits and morphology under light pollution as examples of human-induced rapid environmental change. We show evidence for sex-specific changes in flight-related morphology following development under continuous and dynamic ALAN as well as alterations in mass allocation to thorax muscles and abdomen. Further studies are now warranted to investigate the impact on flight behaviour and fitness.

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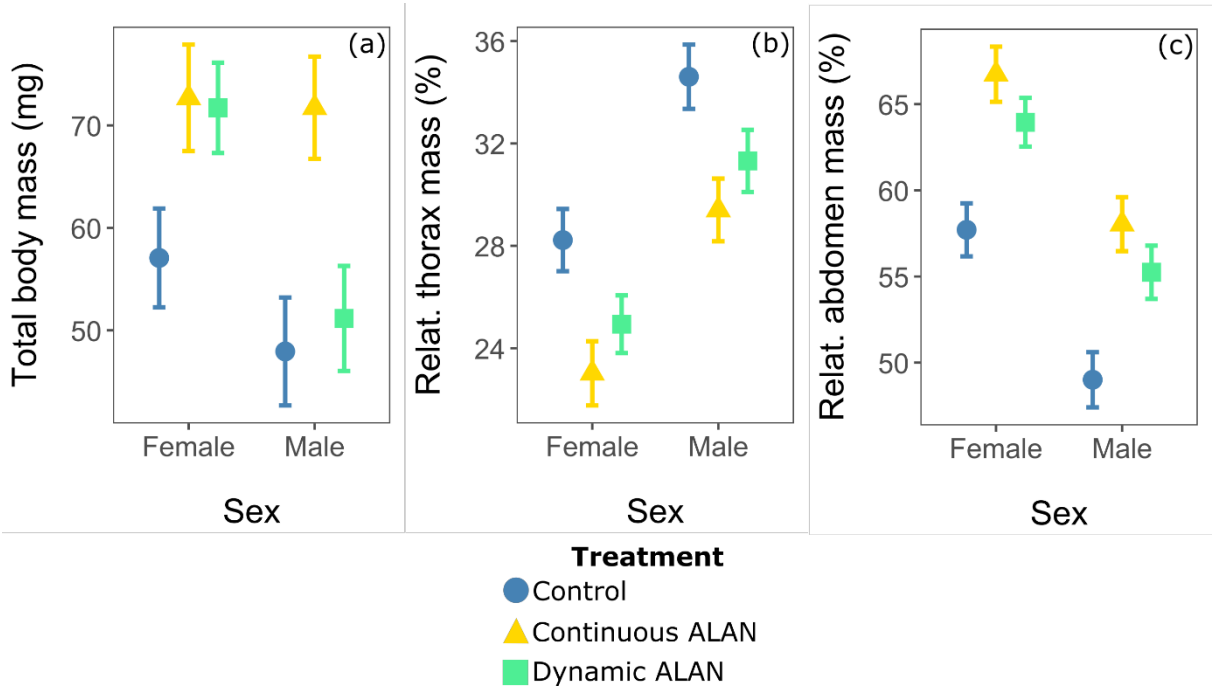
Tables and figures

Table 1 Statistical output of the (generalized) linear mixed models that test differences in flight-related morphology and wing melanisation relative to ALAN treatment, skyglow origin and sex. All tests are based on d.f. = 1, except for treatment effects where d.f. = 2. Significant *p*-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

		χ^2	*p*
Total body mass	Treatment	10.99	**0.004**
	Skyglow	1.02	0.312
	Sex	2.50	0.114
	Treatment x Sex	5.93	0.052°
Relative thorax mass	Treatment	18.60	**< 0.001**
	Skyglow	0.52	0.471
	Sex	42.09	**< 0.001**
Relative abdomen mass	Treatment	31.30	**< 0.001**
	Skyglow	0.11	0.743
	Sex	42.58	**< 0.001**
Forewing length	Treatment	0.088	0.957
	Skyglow	3.61	0.057°
	Sex	2.81	0.093°
	Total body mass	96.54	**< 0.001**
Forewing width	Treatment	2.62	0.270
	Skyglow	1.21	0.271
	Sex	2.83	0.093°
	Total body mass	47.25	**< 0.001**
Forewing area	Treatment	2.61	0.272
	Skyglow	2.38	0.123
	Sex	8.42	**0.004**
	Total body mass	150.96	**< 0.001**
	Treatment x Sex	5.02	0.081°
Forewing aspect ratio	Treatment	1.06	0.588
	Skyglow	0.10	0.750
	Sex	0.81	0.367
	Total body mass	28.30	**< 0.001**
	Skyglow x Sex	4.16	**0.042**
Wing loading	Treatment	0.25	0.882
	Skyglow	0.17	0.678
	Sex	22.57	**< 0.001**
Forewing melanisation	Treatment	4.48	0.106
	Skyglow	1.70	0.193
	Sex	33.63	**< 0.001**
	Skyglow x Sex	3.09	0.079°

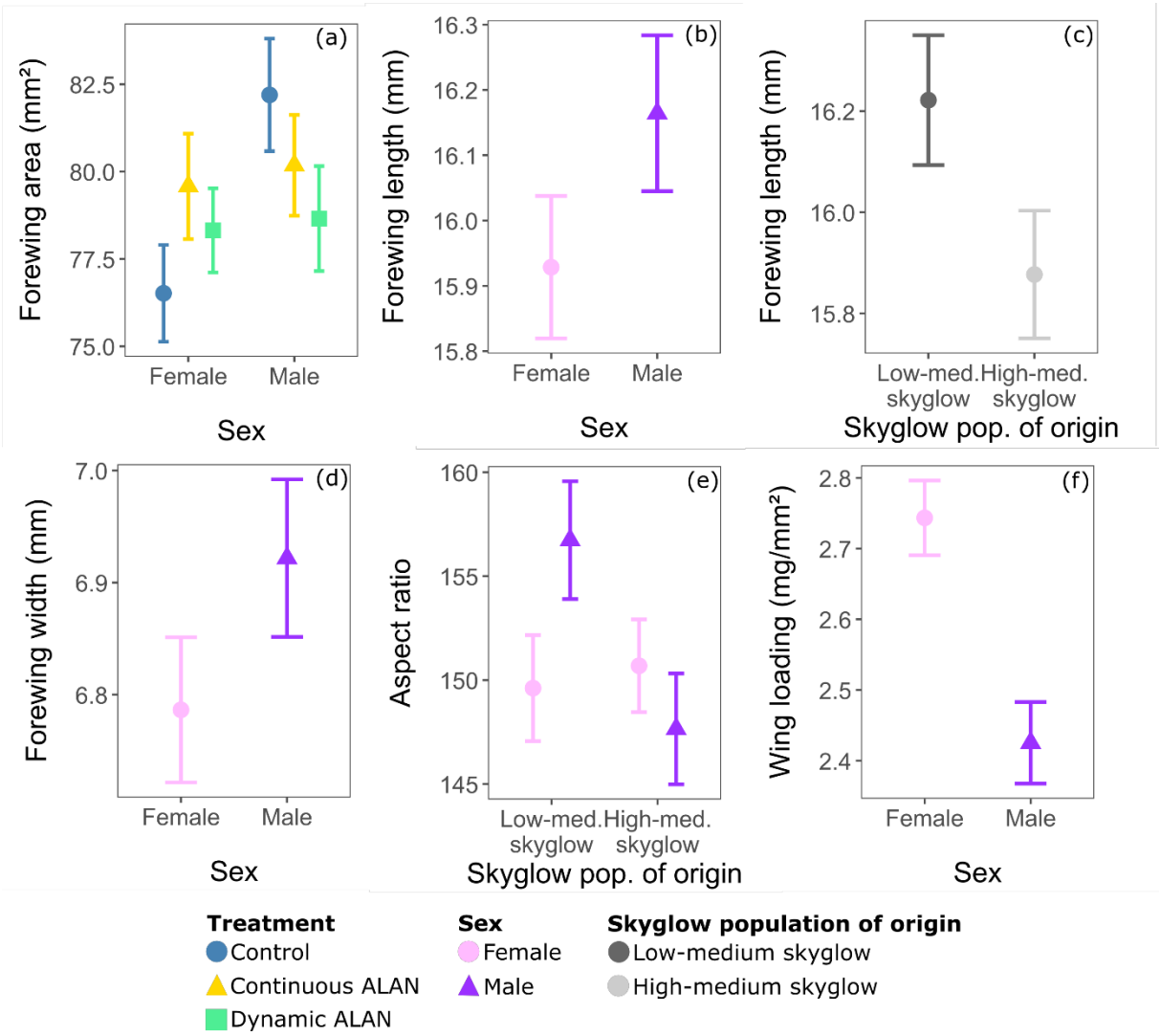


576

577 **Figure 1** Estimated means ± SE of total body mass and relative thorax and abdomen mass in female and

578 male *Agrotis exclamationis* under the three ALAN treatments.

579



580

581 **Figure 2** Estimated means ± SE of wing morphological traits in female and male *Agrotis exclamationis* o

582 riginating from low-medium and high-medium skyglow populations under the three ALAN treatments.

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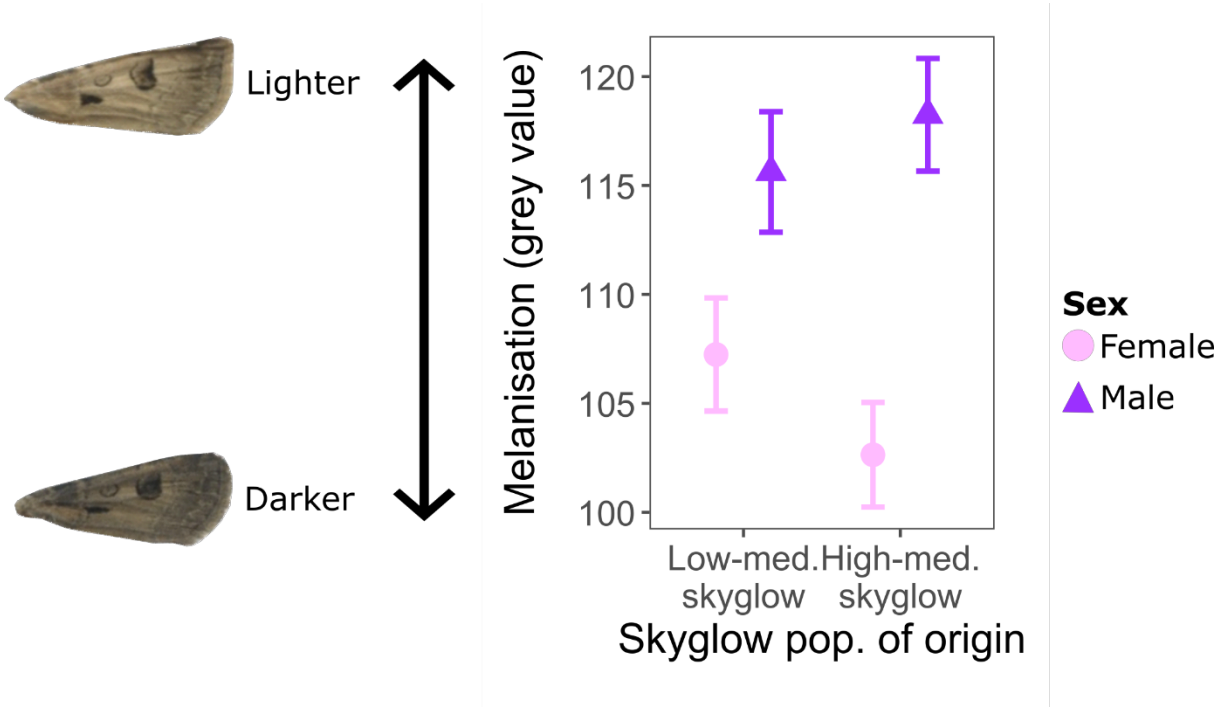

584

585 **Figure 3** Estimated means ± SE of dorsal forewing melanisation in female and male *Agrotis*
586 *exclamationis* originating from low-medium and high-medium skyglow populations. Lower grey values
587 signify darker colour (i.e., higher melanisation).

588

AUTHOR CONTRIBUTIONS

Evert Van de Schoot: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, validation, visualization, writing – original draft, writing – review and editing. **Christophe Pels**: investigation, methodology, validation, writing – review and editing. **Renate A. Wesselingh**: validation, supervision, writing – review and editing. **Hans Van Dyck**: conceptualization, funding acquisition, investigation, methodology, project administration, validation, resources, supervision, writing – review and editing.

DATA AVAILABILITY STATEMENT

The dataset was submitted for peer review at Dryad: http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/p7951Bla7to-P4E28X4azxqPsKDybtr4p7CSgLRDzB8 or https://doi.org/10.5061/dryad.0k6djhbdk

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.