

Moths under bright nights
**Impact of light pollution on development, morphology
and communities**

Evert Van de Schoot
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Université catholique de Louvain | UCLouvain
Earth and Life Institute – Ecology and Biodiversity
Louvain-la-Neuve, Belgium

Supervisor: prof. Hans Van Dyck
Co-supervisor: prof. Renate A. Wesselingh

Members of the examination committee

Prof. Kristof Van Oost (Chairman)

Université catholique de Louvain, Belgium

Prof. Jacqueline Degen

Julius-Maximilians-Universität Würzburg, Germany

Prof. Ruben Evens

Université catholique de Louvain, Belgium

Prof. Dirk Maes

Radboud Universiteit, The Netherlands

Instituut voor Natuur- en Bosonderzoek, Belgium

Prof. Thomas Merckx

Vrije Universiteit Brussel, Belgium

Table of Contents

-----	p. 5	-----
	Summary	
-----		-----
-----	p. 9	-----
	CHAPTER 1	
	General Introduction	
-----		-----
	1.1 Anthropogenic global change	
	1.2 Light pollution as a biodiversity threat	
	1.3 ALAN study system: moths	
	1.4 Larval development under ALAN	
	1.5 The role of flight-related morphology in a light-polluted world	
	1.6 Evolutionary change under ALAN	
	1.7 ALAN as a moth species filter	
	1.8 Objectives and chapter descriptions	
-----		-----
-----	p. 25	-----
	CHAPTER 2	
	Artificial light at night reduces larval survival and constrains female body mass in a capital breeding moth	
-----		-----
-----	p. 45	-----
	CHAPTER 3	
	Experimental study on the impact of continuous and dynamic artificial light at night on moths originating from different skyglow conditions	
-----		-----
-----	p. 67	-----
	CHAPTER 4	
	Evolutionary change in flight-to-light response in urban moths comes with changes in wing morphology	
-----		-----

----- p. 83 -----

CHAPTER 5

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

----- p. 101 -----

CHAPTER 6

Skyglow and especially direct streetlight pollution
alter moth communities

----- p. 135 -----

CHAPTER 7

General Discussion

7.1 Thesis summary and outline of the General discussion

7.2 Moths in light-polluted ecosystems

**7.3 Larval development under ALAN: are some species' ecological profiles
more sensitive than others?**

7.4 Confounding factors

7.5 Recommendations for the planning of public lighting

7.6 Critical notes

7.7 Perspectives: where to go from here?

----- p. 159 -----

Index Lepidoptera species

----- p. 161 -----

References

----- p. 205 -----

Acknowledgements

Summary

Mankind performs an extreme example of niche construction by changing its environment worldwide. This has a direct and indirect global impact on biodiversity. One example of anthropogenic niche construction is the introduction of artificial light at night (ALAN) to extend our activities into the night and increase safety and safety perception. However, this has also resulted in an excess of light in the nocturnal landscape, causing light pollution. Since two decades, ALAN has received increasing attention as a biodiversity threat. Direct light pollution has a local impact and causes a heterogeneous light landscape, while skyglow, caused by the reflection of ALAN by the atmosphere and clouds, is weaker in intensity, but present at a much larger scale. Both types of light pollution affect organisms by disturbing the natural day-night cycle and having a direct impact on behaviour. New lighting technologies that could reduce the impact of ALAN on biodiversity, are being implemented at a large scale, also in Belgium. However, it remains to be seen whether this achieves the intended goal.

Moths are an emblematic study system for the issue of light pollution as most species are nocturnal and are attracted to ALAN, showing the typical flight-to-light response. ALAN not only has a direct impact on adult flight behaviour, but also affects other aspects of their life cycle. *Chapter 1* introduces the known impact of ALAN on larval development and highlights several knowledge gaps. It further discusses how flight-related morphology can play a role in a light-polluted world, the potential for evolutionary changes under ALAN, and how light pollution can affect moth communities by acting as a filter for species and species traits. This PhD thesis has two main objectives to obtain a better understanding of how and why moths are affected by ALAN. First, we want to expand our knowledge on the impact of ALAN on larval development, address its consequences for adult morphology and behaviour and explore the potential for adaptive responses. Second, we aim to investigate how moth diversity and community composition are affected by direct ALAN and skyglow, and explore general patterns in the incidence of ecological species traits under light pollution, independent of species identity.

In *Chapter 2 and 3*, we present evidence for species-specific impacts of ALAN on larval development using split-brood rearing experiments in the lab. First, in *Chapter 2*, larvae of a capital breeding moth with day-active larvae (*Arctia caja*) are reared under either ALAN or control dark conditions. We show evidence for increased larval mortality and acceleration of larval development due to the inhibition of feeding arrest (larval diapause) under

ALAN. Pupal mass decreases under ALAN, but only in females, which can have negative consequences for fecundity. In *Chapter 3*, larvae of two noctuid moth species (*Agrotis exclamationis* and *Ochropleura plecta*) originating from populations under high-medium and low-medium skyglow levels are reared under either dynamic ALAN, continuous ALAN or control dark conditions. The impact of dynamic ALAN is similar, and sometimes even stronger, compared to continuous ALAN. For *A. exclamationis*, we show accelerated larval development and higher growth rate. In contrast to *Chapter 2*, adult body mass increases under ALAN. Qualitatively similar results are shown for *O. plecta*, though less pronounced. No indications for evolutionary change related to development under ALAN are found. These results show that the negative impacts of ALAN on larval development found in most studies cannot simply be extrapolated to all moth species.

In *Chapter 4*, we first explore whether flight-related morphology is related to flight-to-light behaviour. We address whether urban populations of an ermine moth (*Yponomeuta cagnagella*), that had been previously reported to have a weaker flight-to-light response, showed differences in flight-related morphology compared to rural populations. We show evidence for smaller wings in urban moths and this related to the observed reductions in flight-to-light response. Next, in *Chapter 5*, we use *A. exclamationis* specimens from *Chapter 3* to investigate whether larval development under ALAN can result in changed morphology. We measure flight-related morphology, but also relative abdomen mass related to fecundity, and wing melanisation. Development under ALAN result in alterations of sexual size dimorphism due to sex-specific responses in body mass and wing area. We also show evidence for lower aspect ratio in moths originating from populations under high-medium skyglow compared to low-medium skyglow populations, but only in males. Under ALAN, a higher proportion of body mass is allocated to the abdomen and less to the thorax, which could shift the flight-fecundity trade-off. Males originating from high-medium skyglow populations have lighter wings, while females from the same populations have darker wings compared to low-medium skyglow populations, thus increasing the known sexual colour dimorphism.

In *Chapter 6*, we set up a full-factorial study design to simultaneously test the impact of direct light pollution and skyglow on moth communities. In a citizen science project, moths are sampled in gardens with or without direct streetlight pollution in two regions with either low-medium or high-medium skyglow levels. Skyglow has a negative impact on moth abundance, while the presence of streetlights has a stronger negative impact on moth abundance, species richness and diversity. Both skyglow and streetlight pollution change moth community composition. These changes in the local communities are

related to several species life-history and behavioural traits: voltinism, larval food specificity, habitat openness, hibernating stage and larval habitation.

In *Chapter 7*, we discuss the potential consequences of the results obtained in the different chapters of this PhD thesis for moth life histories and behaviour under ALAN, and their interactions with plants and predators in light-polluted ecosystems. Even though the results of *Chapter 2 and 3* have added new knowledge to our understanding of ALAN effects on larval development, it is still unclear whether a species' response can be predicted from certain species traits. This PhD thesis only focusses on the impact of ALAN itself, but in real-world conditions, multiple environmental stressors are simultaneously at play, and here we discuss some of these confounding factors. Based on our results and existing literature, we also make recommendations for the planning of public lighting to reduce the impact of ALAN on biodiversity given the trade-off with human activity and safety perception. Next, we discuss some of our methodological choices made in *Chapter 6*. This PhD work marks a step forward in understanding the impact of ALAN on moths, yet it also underlines how much remains to be done in unravelling its broader ecological consequences and shaping meaningful conservation policies.

CHAPTER 1

General introduction

1.1 Anthropogenic global change

Niche construction is a phenomenon that occurs in various organisms. The definition is broad and exists of two parts (Laland *et al.*, 2016). First, an organism has to significantly modify environmental conditions, usually for its own benefit. Second, these changes have to put selection pressure on the organism itself and several other species. Well-known examples include the complex nests made by social insects, dams constructed by beavers and the alteration of physical and chemical conditions by plants (Day *et al.*, 2003; Odling-Smee *et al.*, 2013). The extreme example of niche construction is performed by our own species *Homo sapiens* (Boivin *et al.*, 2016). Mankind has changed the environment globally, and change occurs at an ever-increasing rate (Steffen *et al.*, 2015; Bruckmeier, 2024). Our impact has led to local and global changes in the abiotic and biotic Earth system (Richardson *et al.*, 2023). Typically, the following five factors are put forward as the most important anthropogenic changes (Bellard *et al.*, 2022): (i) habitat loss and fragmentation due to the conversion of large proportions of natural habitats, mainly for urban and agricultural expansion (Watson *et al.*, 2016; Pardini *et al.*, 2018); (ii) the overexploitation of natural resources in the form of overhunting, -fishing and -harvesting (IPBES, 2022); (iii) the introduction of invasive exotic species (Pyšek *et al.*, 2020); (iv) the release of chemical pollutants (Sigmund *et al.*, 2023) and the alteration of nutrient cycles (e.g., nitrogen: Vitousek *et al.*, 1997 and phosphorus: Yuan *et al.*, 2018); (v) climate change due to fossil fuel burning and land use change (IPCC, 2023). These global changes directly and indirectly affect organisms, resulting in biodiversity changes, including severe losses in all kinds of species groups (e.g., Corlett, 2016; Cowie *et al.*, 2022), including insects (Wagner, 2020). Worryingly, not only rare species but also common species sometimes show strong declines (Gaston & Fuller, 2007; Jansen *et al.*, 2020; van Klink *et al.*, 2024).

Some of these global changes are amplified in urban areas. For instance, the phenomenon of the urban heat island effect leads to locally increased temperatures (Phelan *et al.*, 2015). At night, concrete surfaces slowly release the heat built-up during the day, causing the temperature to drop more slowly. As a result, the urban heat island effect is often stronger at night than during the day (Phelan *et al.*, 2015). After the dominant impact of agriculture, urban expansion is also considered a significant cause of ongoing habitat loss

and fragmentation (Pardini *et al.*, 2018), and many invasive exotic species find suitable habitat in cities to establish their first populations before spreading into the wider countryside (Borden & Flory, 2021). However, urban activities result in many more changes that have often remained under the radar for a long time. An example that has only recently received growing attention is sensory pollution, which can be defined as man-made chemical or physical stimuli that disturb sensory systems of organisms (Dominoni *et al.*, 2020a). In general, the focus lies on three types of such components of human-induced rapid environmental change. First, anthropogenic chemicals can interact with olfactory perception, disrupting plant-pollinator interactions (Jürgens & Bischoff, 2017) and pheromone communication (e.g., Olsén, 2014; Wang *et al.*, 2023). Second, traffic and industrial activities cause noise pollution, interfering with acoustic communication (e.g., Francis *et al.*, 2011; Desjonquères *et al.*, 2020). Third, artificial lighting causes light pollution of the nocturnal environment and living conditions. These three factors can affect biodiversity on their own, but moreover, they often occur together, potentially leading to synergistic or antagonistic effects (as shown in birds: Dominoni *et al.*, 2020b; Ritz-Radlinská *et al.*, 2025). In this PhD thesis, we will focus on light pollution and its impact on different biodiversity aspects, focusing on moths as a study system.

1.2 Light pollution as a biodiversity threat

1.2.1 Artificial light at night

Since the seventeenth century, humans have succeeded in extending human activity in urban areas by introducing public lighting, starting with oil lamps and lanterns (Koslofsky, 2002). The use of public lighting was facilitated by the emergence of gas lighting, where the energy source could be centralised, but it only really gained momentum with the introduction of electric lighting (Holden, 1992). This artificial light at night (ALAN) is part of human niche construction and effectively ensured that social and economic activities could continue during the night and also provided an increased sense of security (Struyf *et al.*, 2019). However, it also spills ‘unnatural’ light that is reflected by aerosols in the atmosphere and clouds, thus lighting the night sky (Falchi *et al.*, 2016). This so-called *skyglow* is often referred to as ‘astronomical light pollution’. A few decades later came the wider realisation that ALAN may affect all kinds of organisms (Verheijen, 1985; Frank, 1988), but it is only since the review by Longcore and Rich (2004) that ALAN has received proper scientific attention as a global change factor relative to biodiversity declines. This ‘ecological light pollution’ consists of both direct

ALAN, originating from streetlights, vehicles, industry, etc., and indirect ALAN from skyglow (Longcore & Rich, 2004). Direct ALAN only has an impact a few dozen metres away from the source, creating a heterogeneous light landscape. On the other hand, skyglow is one to two orders of magnitude weaker in intensity than direct ALAN, but it scatters light over tens to hundreds of kilometres (Falchi *et al.*, 2016). Skyglow is often simply assumed to be homogeneous, but in fact its intensity can vary both spatially (e.g., due to the presence of a large city in one direction: Creemers *et al.*, 2025) and temporally (e.g., due to variation in cloudiness: Kyba *et al.*, 2011). Besides excess light being scattered into the night sky, the light colour or spectrum is also changed. For example, sodium lamps emit yellow/orange light of long wavelengths, while light-emitting diodes (LED) usually emit white light with a high proportion of short wavelengths (i.e., blue light). In this PhD thesis, we will not further elaborate on light spectrum (see Davies *et al.*, 2013; Spoelstra *et al.*, 2015; Alaasam *et al.*, 2021; Corsini *et al.*, 2025), but we will address other aspects of the ecological impact of direct ALAN and skyglow.

More than 80 % of the world population and around a quarter of the land surface experience light pollution (Falchi *et al.*, 2016). Despite increased awareness, this is still growing in area and intensity (Kyba *et al.*, 2017, 2023), including in protected natural areas (Guetté *et al.*, 2018). In the European Union, c. 90 % of the land surface is under light-polluted skies, and due to its high population and road network density, Belgium is one of the hotspots (Falchi *et al.*, 2016; Dekeukeleire *et al.*, 2023). In Belgium, highest light pollution levels are reached in Flanders and the northern part of Wallonia up to the Sambre and Meuse rivers (www.lightpollutionmap.info¹; Fig. 1.1). Only in and around the province of Luxembourg, Viroin-Hermeton and the High Fens weaker light pollution levels are reached, although levels are never completely at zero skyglow or full natural darkness.

¹ Data from 2015

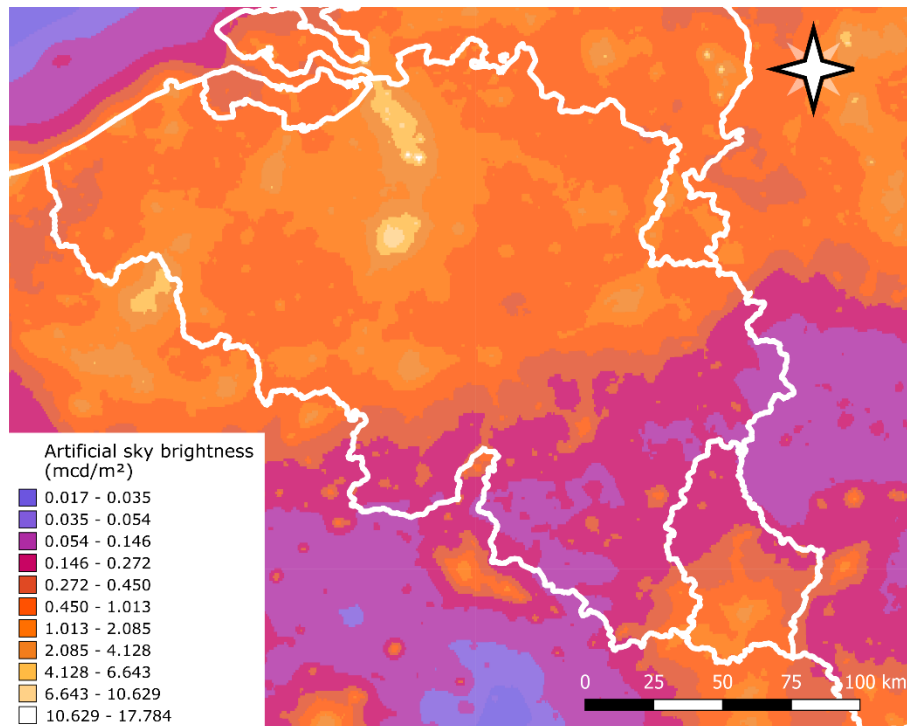


Fig. 1.1. Map showing artificial sky brightness (i.e., skyglow) in Belgium. Blue: low skyglow; purple-red: low-medium skyglow; dark orange: high-medium skyglow; light orange-yellow: high skyglow; white: very high skyglow. Based on data retrieved from Falchi *et al.* (2016).

1.2.2 General effects of ALAN

From animals to plants to fungi, many of these organisms regulate daily physiological and behavioural patterns based on the natural day-night cycle (i.e., circadian rhythm). However, ALAN disrupts this day-night cycle by increasing nocturnal light levels by 10 to 1000 times and can therefore affect biological timings (Gaston *et al.*, 2017). As a result, diurnal or crepuscular species can prolong their activity period (e.g., Raap *et al.*, 2015; Pulgar *et al.*, 2019), while the opposite can be true for nocturnal species (e.g., Le Tallec *et al.*, 2013; Duarte *et al.*, 2019). Moreover, ALAN disturbs the induction of sleep (e.g., through the suppression of melanin production: Jones *et al.*, 2015; Aulsebrook *et al.*, 2018; Grubisic *et al.*, 2019), which can lead to increased stress (Nollet *et al.*, 2020; Vaccaro *et al.*, 2020). Further, crepuscular and especially nocturnal animals are adapted to see at low light

levels, usually with very sensitive photoreceptors. But also here, an excess of ALAN can interfere with visual cues (Davies *et al.*, 2013).

Many animals use celestial cues for orientation during migration (e.g., birds: Wiltschko & Wiltschko, 2015, dung beetles: Dacke *et al.*, 2021 and moths: Sotthibandhu & Baker, 1979; Warrant *et al.*, 2024). However, skyglow can reduce the visibility of these cues, this way leading them from the right track (Torres *et al.*, 2020; Warrant *et al.*, 2024). Furthermore, in insects, celestial light is used to maintain proper body orientation by keeping their dorsal side facing the sky light. However, they also exhibit this same behaviour in the vicinity of point sources of ALAN, resulting in the typical flight-to-light response (Fabian *et al.*, 2024). In contrast, skyglow does not affect body orientation, because it comes from the same direction as celestial light. The flight-to-light response affects mating (van Geffen *et al.*, 2015b; Botha *et al.*, 2017; McLay *et al.*, 2018; Storms *et al.*, 2025) and feeding behaviour (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022), and can increase the risk of being preyed upon (Willmott *et al.*, 2019; Hügél & Goerlitz, 2020; Hermans *et al.*, 2024).

1.2.3 New streetlight technologies and their deployment in Belgium

With our pursuit of higher energy efficiency, lighting technologies are constantly evolving and the development of LEDs has strongly accelerated this (Olajiga *et al.*, 2024). In Flanders, 84 % of regional road lighting and 43 % of highway lighting has been converted to LEDs (www.wegenenverkeer.be; Dekeukeleire *et al.*, 2023), while in Wallonia, this is 70 % and 80 %, respectively (www.wallonie.be). Despite the fact that the cheapness of LEDs can be misused to install more public lighting (Kyba *et al.*, 2017), some of these developments could also prove useful for reducing the impact of ALAN on biodiversity (Owens *et al.*, 2024). First, LED light beams can be more precisely targeted downwards in order to avoid spilling beyond the area of interest. This measure has been shown to effectively reduce flight-to-light by insects (Bolliger *et al.*, 2020; Dietenberger *et al.*, 2024), but see van Koppenhagen *et al.*, 2024). A second benefit of LEDs is that their light spectrum can be more easily modified, which made it possible to create so called 'bat-friendly' lighting. This lighting is red or amber and minimizes the impact on bats (e.g., Spoelstra *et al.*, 2017), but the impact on invertebrates is variable (van Geffen *et al.*, 2014; van Grunsven *et al.*, 2020; Kivelä *et al.*, 2023; Spoelstra *et al.*, 2023; Corsini *et al.*, 2025). Finally, the intensity of LED streetlights can be adjusted to the amount of passing traffic. This results in ALAN varying in intensity throughout the night, which is here referred to as dynamic ALAN. In this regard, streetlights can be either partially or fully dimmed at times of low traffic volume. Partial dimming results in a reduction of ALAN intensity during part of the night and has been shown to reduce

attractivity for insect and bats (Bolliger *et al.*, 2020). Full dimming reduces the exposure time to ALAN and could therefore be expected to have a lower impact on biodiversity compared to full-night ALAN. Dimming can be set at a fixed time period of lower traffic volumes. In Flanders, 40 % of the highway lighting consists of such dynamic streetlights (www.wegenenverkeer.be), while in Wallonia, this is already 80 % with full dimming on highways and 70 % with partial dimming on regional roads (www.wallonie.be). Another type of dynamic lighting are 'smart lights' with motion detection that switch on when someone is passing by and switch off again after a short amount of time. This type is often used for illuminating small roads that are typically reserved for pedestrians and cyclists, but it is also used as a porch light. In our experiments we will refer to dynamic ALAN as pulsed ALAN that simulates this kind of lighting with motion detection. So far, the impact of dynamic ALAN has only been little studied, but two studies showed an impact that is at least as strong as full-night ALAN (Heinen *et al.*, 2023; Fabusova *et al.*, 2024), potentially because this kind of dynamic ALAN also lowers the predictability of ALAN exposure (Owens *et al.*, 2024).

1.3 ALAN study system: moths

1.3.1 Moth ecology

One of the most studied groups of organisms in light pollution research are moths (Heterocera). Moths form a paraphyletic group of insects that contains all Lepidoptera that do not belong to the monophyletic group of the butterflies (Rhopalocera or Papilionoidea) (van Nieukerken *et al.*, 2011). Historically, the group is subdivided into macro- (Macrolepidoptera) and micro-moths (Microlepidoptera). However, from a phylogenetic point-of-view these clades are artificial (van Nieukerken *et al.*, 2011), based on the body size of most species within the families they contain. Moths are holometabolous insects, meaning that their life cycle consists of the following stages: eggs, several larval stages or instars, pupae and adults or imagines. The larvae exhibit a wide variety of life styles in terms of feeding behaviour (Sterling *et al.*, 2012; Waring *et al.*, 2015): (i) larvae can be found feeding from woody to herbaceous plants, from mosses to lichens and fungi and from stored grain products to dead animal and plant matter. Some moth species only feed on one very specific food source, while other species show no preference at all; (ii) feeding can take place from a variety of habitations; larvae can live openly on the food source, in a rolled-up leaf, within a stem, in a leaf mine, underground, etc., and this can even vary among larval stages and/or generations (e.g., the first generation larvae of the triangle plume

Platyptilia gonodactyla (Pterophoridae) start feeding in the roots of *Tussilago farfara* and then eat their way through the stem towards the flower heads; the second generation first mines the leaves and later lives openly on the underside of the leaf). In adult moths, there are different strategies in terms of nutrient acquisition for reproduction (Tanmaru & Haukioja, 1996). The so-called capital breeders fully rely on the nutrients consumed during the larval stage and usually do not feed as an adult. On the other hand, income breeders do feed in the adult stage and rely at least partially on these nutrients for egg production.

1.3.2 Moths and ecosystem functioning

Many people see moths as pest species causing yield losses, infesting stored food products, damaging clothes or causing nuisance through urticating setae. For example, the moth *Plutella xylostella* is estimated to cause an annual cost of US\$4 billion–US\$5 billion (Zalucki *et al.*, 2012). However, such negative impacts concern only a small proportion of the moth species (New, 2004; Sterling *et al.*, 2012; Waring *et al.*, 2015). On the contrary, they fulfil essential ecosystem roles in interactions with plants and predators. First of all, all moth stages serve as a food source for various other animals. For example, parasitoid flies and wasps parasitize eggs, larvae and pupae (e.g., Mills, 2005); small songbirds like *Parus major* rely for a great part on moth larvae during the nesting season (Coomes *et al.*, 2024); and many bats hunt to a greater or lesser extent for adult moths (ter Hofstede & Ratcliffe, 2016).

Secondly, moths make a significant contribution to plant pollination. Some plant species are exclusively visited by moths (for examples, see Hahn & Brühl, 2016), while in common plants like *Silene latifolia*, *Rubus* sp. and *Trifolium pratense*, pollination by moths is at least complementary to diurnal pollinators (Giavi *et al.*, 2020; Alison *et al.*, 2022; Anderson *et al.*, 2023). Moreover, recent evidence shows that crops like strawberries and blueberries are also partially pollinated by moths (Fijen *et al.*, 2023; Buxton *et al.*, 2025). Moths also show interactions with plant microorganisms. For example, leaf-feeding moth larvae in trees have been shown to facilitate the presence of phyllosphere microbes like bacteria and yeasts (Stadler & Müller, 2000). Furthermore, adult moths can serve as vectors for nectar microbes (Feldman *et al.*, 2008; Ma *et al.*, 2025). These microbes (e.g., yeasts, fungi and bacteria) can alter the nutritional composition of nectar, but also its flavour and scent, and their dispersal by moths and other pollinators can thus, positively or negatively, affect the broader pollinator community (Martin *et al.*, 2022).

Finally, moths also provide cultural ecosystem services for mankind (Duffus *et al.*, 2021). They are not only used as a study system to address ecological issues (Uhl *et al.*, 2022), but also in art, mythology, movies and

literature. For example, moths are often metaphorically associated with death, but also rebirth and transformation due to their complete metamorphosis as in the film 'The Silence of the Lambs' (Cherry, 2011; Van Huis, 2019). However, artists also depicted moths just for aesthetic reasons, and some also combined art with science. For example, artists like Maria Sibylla Merian have carefully observed and described the life cycle of moths and even their parasites using drawings (Etheridge, 2011). Furthermore, silk-producing moths (e.g., *Bombyx mori*) also play a significant role in fashion culture (Takeda, 2009).

1.3.3 Moths: conservation status and threats

Thus far, the vast majority of studies on moth trends has focused on Europe, more specifically Western, Northern and Central Europe (Groenendijk & Ellis, 2011; Valtonen *et al.*, 2017; Antão *et al.*, 2020; Fox *et al.*, 2021; Burner *et al.*, 2021; Veraghtert *et al.*, 2023; Yazdanian *et al.*, 2023). Only recently, studies from other regions have appeared (e.g., the Americas: Salcido *et al.*, 2020; Wagner *et al.*, 2021 and South Korea: Kwon *et al.*, 2024). The trends shown in these studies are heterogeneous, with significant declines in moth abundance and species richness mainly being found in areas under strong pressure of human activities (Groenendijk & Ellis, 2011; Valtonen *et al.*, 2017; Antão *et al.*, 2020; Fox *et al.*, 2021; Burner *et al.*, 2021; Veraghtert *et al.*, 2023; Kwon *et al.*, 2024, but see Salcido *et al.*, 2020), while areas with low anthropogenic activity show no clear trends (Wagner *et al.*, 2021; Yazdanian *et al.*, 2023).

Changes in moth diversity are caused by a 'cocktail' of environmental stressors that does not take a single form. Habitat destruction due to land use change (i.e., deforestation, agricultural intensification, urbanisation, etc.) and chemical pollution (e.g., pesticides and eutrophication) probably have the largest negative impact on moth populations (Fox, 2013; Wagner *et al.*, 2021). The effects of climate change go in two directions. On the one hand, it can lead to range expansion in moth species adapted to warmer climates (Mason *et al.*, 2015; Antão *et al.*, 2020; Fox *et al.*, 2021), but on the other hand, species that cannot shift their ranges show severe population declines or go (locally) extinct (Martay *et al.*, 2017). The fact that most moth species are nocturnal and, to a greater or lesser extent, show a flight-to-light response, has resulted in an increased focus on light pollution as a possible driver of moth declines (van Langevelde *et al.*, 2018; Boyes *et al.*, 2021a). Although studies directly linking moth population trends to light pollution are still lacking, evidence is compiling on the disturbing impact of ALAN on adult flight (Degen *et al.*, 2024; Fabian *et al.*, 2024), feeding (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022) and mating behaviour (van Geffen *et al.*, 2015b, 2015a; Cieraad *et al.*, 2022; Storms *et al.*, 2025), but also on larval

development (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Schroer *et al.*, 2019; Merckx *et al.*, 2023). In *section 1.4*, we will elaborate on the known effects of ALAN on larval development in moths and indicate knowledge gaps regarding this issue.

1.4 Larval development under artificial light at night

Larvae are the main feeding stage of insects and their ontogeny determines largely the resource capital and body size of the adults. Multiple aspects of larval development are regulated by natural light cycles, often in combination with temperature (Saunders, 2009). In Lepidoptera, for example, photoperiod is related to larval activity (Lance *et al.*, 1986), development time (Leimar, 1996; Pavan *et al.*, 2010; Hasan *et al.*, 2020), diapause induction (Roditakis & Karandinos, 2001; Hasan *et al.*, 2020; Numata & Shintani, 2023) and final body size (Leimar, 1996; Pavan *et al.*, 2010). Furthermore, moth larvae can show both positive and negative phototactic behaviour, which can also vary throughout development (Beetsma *et al.*, 1962; Griswold & Trumble, 1985). Therefore, larval development has a strong potential to be affected by ALAN. Indeed, previous studies on larval development under ALAN in moths and the butterfly *Danaus plexippus* have shown altered feeding activity (Haynes *et al.*, 2023), faster larval development (van Geffen *et al.*, 2014; Merckx *et al.*, 2023), diapause inhibition (van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Merckx *et al.*, 2023), lower growth rate (Grenis & Murphy, 2019) and decreased body mass (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023).

These results suggest that ALAN mainly has a negative impact on larval development in moths. However, several knowledge gaps regarding this issue still remain. First, most of the moth species in these previous studies feed on nectar as adults, and could therefore, at least partially, compensate for lower built-up of resource capital during larval development (i.e., income breeders: Tammaru & Haukioja, 1996). A considerable proportion of moth species can be defined as capital breeders, which do not feed as adults (in Belgium at least one in six macro-moth species: Maes *et al.*, 2024), and thus do not have this possibility of compensation. Consequences for the adult stage could therefore be expected to be stronger in species with this life-history strategy. Second, ALAN can be expected to disrupt feeding behaviour in species that have larvae with a nocturnal activity peak, which may explain its negative effects (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023). In contrast, ALAN may extend the active period of diurnal caterpillars into the night, which can be expected to have a positive impact on larval development; however, this has not been tested so far. Third, it

remains to be investigated whether the lower exposure time provided by dynamic ALAN compared to continuous ALAN also results in a weaker effect on larval development. Finally, environmental conditions during larval development can alter adult morphology. In *section 1.5*, we will further discuss the potential implications of this with regard to light pollution.

1.5 The role of flight-related morphology in a light-polluted world

Flight-to-light is one of most well-known behaviours of adult moths (Fabian *et al.*, 2024). This can draw them away from suitable habitat (Frank, 2006), and as mentioned earlier, it can disrupt mating (van Geffen *et al.*, 2015b, 2015a; Cieraad *et al.*, 2022; Storms *et al.*, 2025) and feeding behaviour (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022) and increase the risk of predation (Wakefield *et al.*, 2015; Willmott *et al.*, 2019). In populations where a sufficient proportion of the individuals experience these negative effects, there is scope for an evolutionary response to reduce flight-to-light (Hopkins *et al.*, 2018). Indeed, Altermatt and Ebert (2016) found that *Yponomeuta cagnagella* populations originating from urban light-polluted areas showed a lower flight-to-light response than conspecifics from rural dark areas. The authors suggested that these results could be related to differences in overall flight mobility or performance, as this could lower the chance of ending up in the attraction zone of an artificial light source (Truxa & Fiedler, 2012; Merckx & Slade, 2014; Degen *et al.*, 2024). Flight performance in insects can be tested in tethered flight experiments (Jones *et al.*, 2016; Minter *et al.*, 2018), but it is more easily estimated by using flight-related morphology as a proxy (e.g., Berwaerts *et al.*, 2002). For example, increased mass allocation towards flight muscles and larger wings are associated with higher flight performance (Berwaerts *et al.*, 2002; Jyothi *et al.*, 2021), while lower wing loading (i.e., body mass divided by wing area) is related to increased manoeuvrability (Le Roy *et al.*, 2019). Therefore, in populations with a reduced flight-to-light response, we would expect to find individuals with lower relative thorax mass and smaller wings.

Multiple studies have shown that environmental conditions experienced during larval development can determine flight-related morphology at the adult stage (food quality: Pellegrons *et al.*, 2009; Gibbs *et al.*, 2012, temperature: Frazier *et al.*, 2008 and predation: Kahnt *et al.*, 2025). ALAN has been shown to reduce body mass (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023), but the impact on flight-related morphology is currently unknown. However, it would be interesting to investigate such effects as this can have consequences for flight performance and, potentially, flight-to-light behaviour.

1.6 Evolutionary change under ALAN

It is clear that ALAN can affect moths and other organisms in various ways, sometimes positively, but mainly negatively. As mentioned in *section 1.5*, when a significant proportion of a population experiences a positive or negative fitness impact from ALAN, this opens perspectives for adaptive evolution to, respectively, enhance or reduce ALAN effects (Hopkins *et al.*, 2018). However, only very little evidence for such adaptations has been provided, so far (Candolin, 2024). In insects, the only example is the reduced flight-to-light response in *Y. cagnagella* moths originating from light-polluted urban areas (Altermatt & Ebert, 2016). However, it should be noted that this study only tested F_1 - individuals, and thus did not perform a common-garden experiment with F_2 -individuals to disentangle genetic and maternal effects. It has not yet been properly tested whether this phenomenon is more widespread, but two studies showed some indications. Ground beetles (Carabidae) caught in cities were less attracted to light than beetles from dark sky reserves (Kaunath & Eccard, 2022); and in the moth *Helicoverpa zea*, the ratio between light and pheromone-trapped specimens is decreasing over time, suggesting that the flight-to-light response is decreasing in this species (Battles *et al.*, 2024). One other study in *Y. cagnagella* investigated whether populations under direct light pollution also showed an adaptive response for adult feeding and mate calling, but they found no indications for this (Cieraad *et al.*, 2022). It should be noted that the collection sites in this study were all located under high to very high skyglow levels, which may mask effects of direct ALAN (Dickerson *et al.*, 2022). Therefore, sampling populations in high *versus* low skyglow areas (*cf.* Altermatt & Ebert, 2016) is more appropriate for this kind of studies. Potential adaptive responses in other traits have not yet been tested. However, it would be interesting to test for changes in, for example, larval development. Given the negative impact of ALAN on larval development, evolutionary changes in behavioural and physiological responses could reduce body mass loss or diapause inhibition.

1.7 ALAN as a moth species filter

Experimental studies showing evidence on the effects of ALAN in single moth species is compiling (Boyes *et al.*, 2021a). However, the impact on moth communities are hard to predict from such studies alone. First, different species do not respond to ALAN in the same way or to the same extent (e.g., in terms of flight-to-light behaviour: van Langevelde *et al.*, 2011; Merckx & Slade, 2014). Furthermore, the outcome of species interactions like

competition and predator-prey relationships also play an important role in determining community composition (Cadotte & Tucker, 2017). Studies comparing communities in light-polluted and dark areas could provide insights in the way ALAN acts as a species filter (Sanders & Gaston, 2018). However, to obtain a more generalizable understanding of how ALAN affects community composition, independent of species identity, it is interesting to also investigate the incidence of species traits (Zakharova *et al.*, 2019; Green *et al.*, 2022).

Moths can respond quickly to differences in environmental conditions (e.g., Uhl *et al.*, 2022) and their diversity and their morphological and life-history traits are especially well-documented in Northern, Western and Central Europe (Franzén & Betzholtz, 2012; van Langevelde *et al.*, 2018; Maes *et al.*, 2024). Moreover, methods for moth sampling require relatively low effort and can be easily standardized. Therefore, moths are often used in these regions to investigate the impact of environmental changes on biodiversity (e.g., in the context of urbanisation: Merckx *et al.*, 2018; Franzén *et al.*, 2020; Belitz *et al.*, 2024; Vähätalo *et al.*, 2024). So far, only two studies have investigated the impact of light pollution on moth communities (Grenis *et al.*, 2023; Sanetra *et al.*, 2024). However, in both studies, it was hard to distinguish direct ALAN and skyglow effects from other urbanisation-related effects due to high correlation. Moreover, species traits were not assessed in both these studies. This leaves scope for trait-based moth community studies that can effectively separate the impact of direct ALAN and skyglow, independent of urbanisation context.

1.8 Objectives and chapter descriptions

For this PhD thesis, we have identified two overarching research objectives. The first one will focus on single-species effects of ALAN, while the second relates to the impact of ALAN on moth communities.

1.8.1 First main research objective: species-specific impact

Studies investigating effects of continuous ALAN on larval development in moths have only focused on income breeding species with nocturnal larvae that belong to two families (Noctuidae: van Geffen *et al.*, 2014; Grenis & Murphy, 2019 and Geometridae: Merckx *et al.*, 2023). Therefore, there is a need for studies that use species with different life-history strategies and larval activity patterns, and investigate the impact of new streetlight technologies. Furthermore, it is still unclear whether larval development under ALAN conditions changes adult morphology and whether the latter is related to differences in flight-to-light behaviour. Finally, it would be

interesting to test whether moth populations originating from areas with strong light pollution show an evolutionary response that reduces negative effects or enhances positive effects on ALAN on larval development (as shown for flight-to-light behaviour: Altermatt & Ebert, 2016). The first goal of this PhD thesis is to expand our knowledge on the impact of ALAN on larval development, investigate the consequences for adult morphology and behaviour and explore indications for evolutionary responses.

1.8.2 Second main research objective: community-level impact

Direct ALAN from public lighting results in a heterogeneous light landscape at night and affects moths at a local scale, while indirect ALAN from skyglow can put chronic pressure on moths over an area of tens to hundreds of kilometres (Falchi *et al.*, 2016; Boyes *et al.*, 2021a). Both types of light pollution can occur simultaneously, but so far, it has remained largely unclear how they affect moth communities. The designs of the two studies that have investigated the impact of light pollution on moth diversity and community composition did not allow to disentangle effects of direct ALAN, skyglow and urbanisation due to strong correlation between these factors (Grenis *et al.*, 2023; Sanetra *et al.*, 2024). Moreover, these studies only focused on the impact of light pollution on moth diversity and community composition, but they did not use trait-based analyses to investigate more generalizable patterns of how moth communities are affected. The second goal of this PhD thesis is to investigate the impact of direct ALAN and skyglow on moth diversity and community composition, and to explore patterns in the incidence of species life-history and behavioural traits in the communities under light pollution, independent of species identity, in a study design that allows for proper simultaneous testing of both types of light pollution.

1.8.3 Chapter overview

Below, we give a brief summary of the different chapters of this PhD thesis as well as their respective contributions to the overall aims of this work. A schematic overview of the main research objectives as well as a description of the different chapters and how they relate to each other, is shown in Fig. 1.2.

- In **Chapter 2**, we investigate the effects of continuous ALAN on larval development in a capital breeding moth that has larvae with a diurnal activity peak (*Arctia caja*, Erebidæ). During this experiment that runs for two generations, we monitor larval survival, feeding frequency, development time and induction of feeding arrest (i.e., diapause). Pupal mass was used as a proxy for final body mass.

- **Chapter 3** focusses on the impact of new lighting technologies on larval development. Larvae of two common moth species (*Agrotis exclamationis* and *Ochropleura plecta*, Noctuidae), originating from populations that experience different skyglow levels, are exposed to continuous and (smart streetlight-like) dynamic ALAN, in order to test for both plastic constraints and evolutionary responses. We monitor larval survival, feeding behaviour, development time and growth rate as well as final body mass.
- In **Chapter 4**, we assess whether flight-related morphology is related to flight-to-light behaviour. Altermatt and Ebert (2016) showed evidence for a reduced flight-to-light response in moths originating from urban light-polluted areas. Using the same specimens, we test whether flight-related morphology differs between urban and rural populations, and whether these changes are related to the observed changes in flight-to-light-response.
- **Chapter 5** elaborates on the rearing experiment in *Chapter 3* and uses the insights of *Chapter 4*. We investigate whether larval development under continuous and dynamic ALAN results in changed flight-related morphology, and whether responses are sex-specific, leading to alterations in sexual dimorphism.
- In **Chapter 6**, we study the impact of direct streetlight pollution and skyglow on moth communities. In two Belgian regions with significantly different skyglow levels, moths are sampled in citizen-scientist gardens that are either dark or illuminated by streetlight, creating a full-factorial study design. We test for effects on moth abundance, species richness, diversity and community composition. Furthermore, we assess the presence of general patterns in a species trait-based analysis, using a community-weighted means approach.
- Finally, in **Chapter 7**, we give a summary of our results and discuss the consequences for moths and the organisms they interact with in light-polluted ecosystems. We also discuss the role of species traits related to larval development under ALAN. Further, we give an overview of potential confounding factors, and we make recommendations for the planning of public lighting. To conclude, we reflect on perspectives for future research.

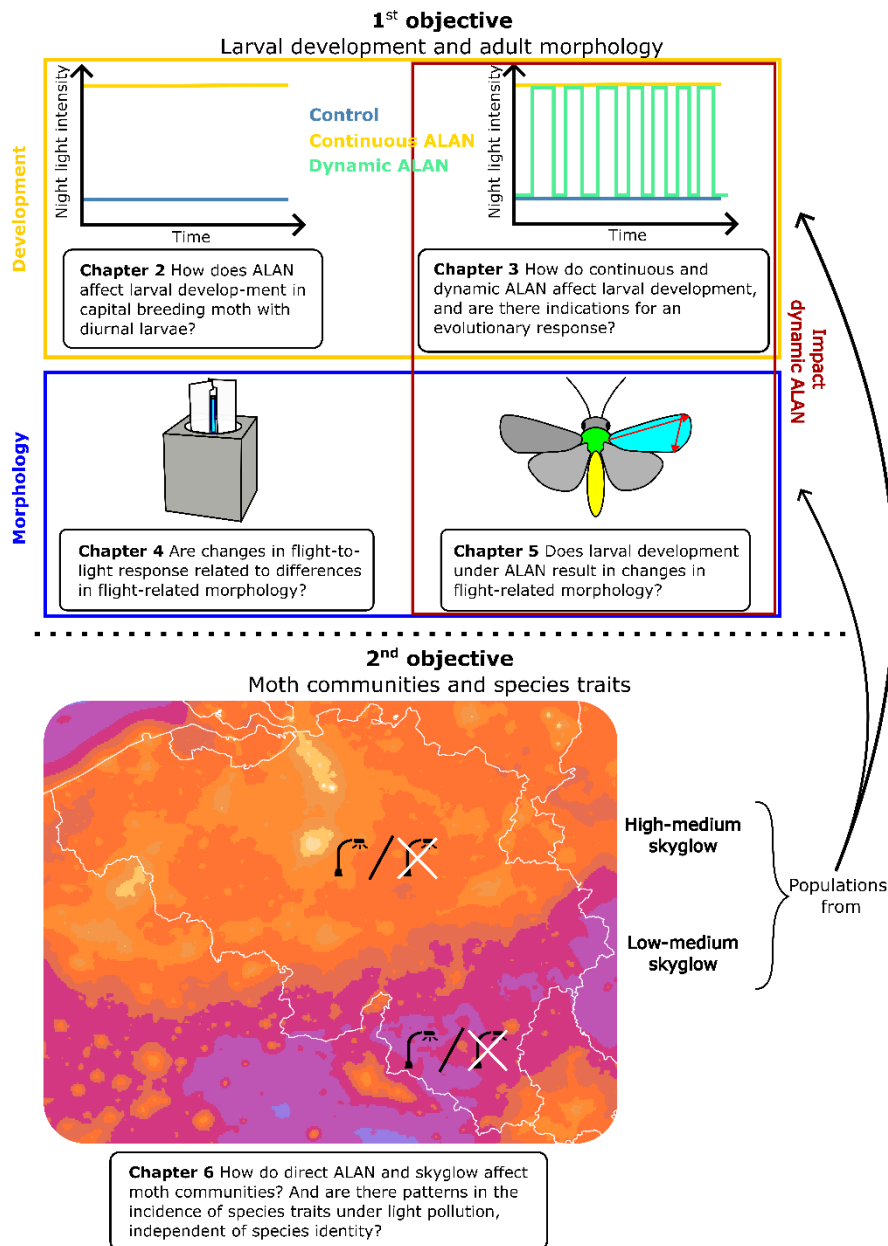


Fig. 1.2. Schematic overview of the research questions addressed in the chapters of this PhD thesis. *Chapter 2 and 3* address ALAN effects on larval development. *Chapter 4* investigates relationships between flight-related morphology and flight-to-light. In *Chapter 5*, the impact of larval development under ALAN on morphology is tested. *Chapter 6* concerns a study on the impact of skyglow and direct light pollution in moth communities.

CHAPTER 2

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

Authors: Evert Van de Schoot, Renate A. Wesselingh and Hans Van Dyck

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In this chapter, we investigate the impact of ALAN on larval survival and development and consequences for pupal mass in a tiger moth with an understudied ecological profile regarding this issue, namely a capital breeder with diurnal larvae.

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 F₁ and F₂ 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 F₁ and F₂ 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 (Sotthibandhu & Baker, 1979; Dacke *et al.*, 2021), 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 (van Geffen *et al.*, 2015b; Botha *et al.*, 2017) as well as feeding behaviour (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022).

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 (van Geffen *et al.*, 2014; Merckx *et al.*, 2023) and lower body mass (van Geffen *et al.*, 2014; Grenis & Murphy, 2019). There is also evidence for the disruption of diapause induction (van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Merckx *et al.*, 2023), 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 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 (van Geffen *et al.*, 2014; Durrant *et al.*, 2018; Grenis & Murphy, 2019; Merckx *et al.*, 2023). 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 (Lamunyon, 1997; Heisswolf *et al.*, 2009). Our experimental test was conducted with both F₁ and F₂ 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., F₁ 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 F₂ generation larvae, which resulted from crossbreeding between males and females of the different families in the F₁ 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 x 18.5 x 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 boxes² with several 1-mm holes for aeration, a piece of paper towel, and in the F₁ experiment with a metal grid (1 x 1 mm) 1 cm above the bottom of the box. Diurnal light was provided by VEGELED LO250 floodlights (Colasse, 4000K; 80000 lx; Fig. S2.1, Appendix C2). Every

² 11.5 x 11.5 x 6 cm, polystyrene, Biopack

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.

F₁ generation

Offspring of wild-caught females ($N = 3$) were reared in a single climate chamber under a day-night cycle of LD 15:9 ($T_{\text{day}} = 21^{\circ}\text{C}$, $T_{\text{night}} = 16^{\circ}\text{C}$). 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 lx; measured in ten random rearing boxes per treatment with a Brannan Light Meter; Fig. S2.2, Appendix C2). An equal number of larvae experienced control dark nights (0.40–0.63 lx). 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. S2.3, Appendix C2). 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. S2.4, Appendix C2). 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. S2.5, Appendix C2). To produce the F₂ generation, non-related F₁ males and females grown under the control treatment (i.e., experimental individuals 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.

F₂ generation

In total, 14 F₂ 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 lx) and the other half received ALAN from one LED light (Philips 1.4 W, 2700 K; 9.10–31.97 lx). 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 F₁ experiment (Fig. S2.6, Appendix C2). 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 S2.5, Appendix C2).

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 F₂ 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 F₁ generation, and with a GLMM with a binomial error distribution for the F₂ generation. Effects of sex, treatment (and feeding frequency for the F₂ 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 Appendix C2 (Table S2.1-2.2) as well as sample sizes (Table S2.3). 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 2.1). 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. 2.1), and they mainly did in the final larval stages, while under the control treatment, they mainly did so at the hibernating stages (Fig. S2.7, Appendix C2). 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 2.1). Mortality rate was especially higher between day 150 and 200 (treatment: $\chi^2 = 9.66$, $p = 0.002$; Fig. 2.1).

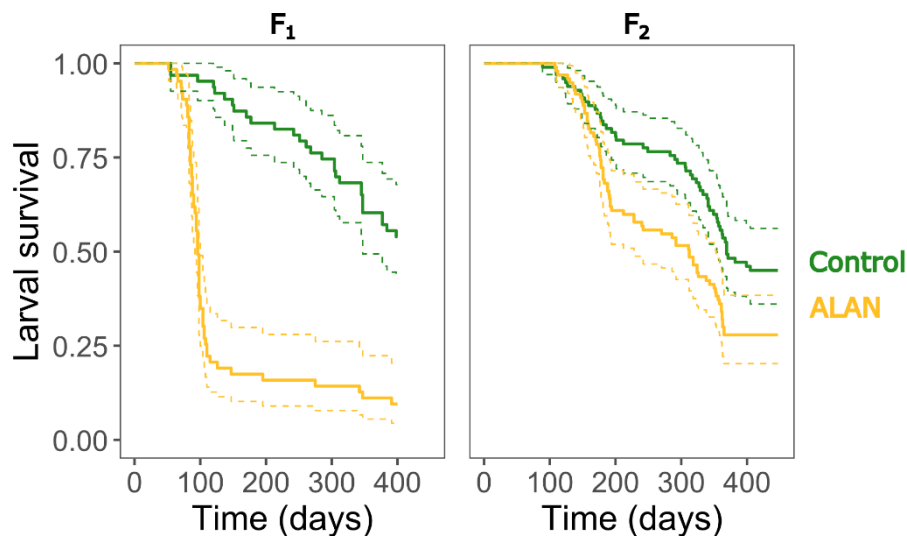


Fig. 2.1. Larval survival curves and 95 % confidence intervals (broken lines) under the control and ALAN treatment for the F_1 and F_2 generation.

Development

In the F₁ generation all individuals in the control treatment showed a feeding arrest, while this was the case for only one female in the ALAN treatment³ (Table 2.1; Fig. 2.2a). As a consequence, larval development was on average 51.8 % shorter under the ALAN treatment than under the control treatment (Table 2.1; Fig. 2.2b). There was also moderate evidence for sexual dimorphism in pupal development time, since males took 15.8 % more time to develop than females (Table 2.1; Fig. 2.2c). In the F₂ generation, under the ALAN and control treatment, 11.1 and 80.0 % ⁴of the females, respectively, showed a feeding arrest, while in males this was 38.9 and 59.1 %⁵, respectively (Table 2.1; Fig. 2.2a). The larval stage lasted longer under ALAN than under the control treatment at a low feeding frequency, but shorter at high feeding frequency (Table 2.1; Fig. 2.2b). Under the ALAN treatment, pupal development was 11.1 % shorter compared to the control treatment (Table 2.1; Fig. 2.2c).

Body mass

For the F₁ 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 2.1; Fig. 2.2d). 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 2.1; Fig. 2.2f). In females of the F₂ 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 2.1; Fig. 2.2d-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 2.1; Fig. 2.2f).

³ Control: 35/35, ALAN: 1/7

⁴ Female control: 16/20, ALAN: 1/9

⁵ Male control: 13/22, ALAN: 7/18

Table 2.1. Statistical output for differences in mortality and development in the F₁ and F₂ 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 Feeding frequency	3.26	0.071°
				Treatment		
				Sex x Treatment 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

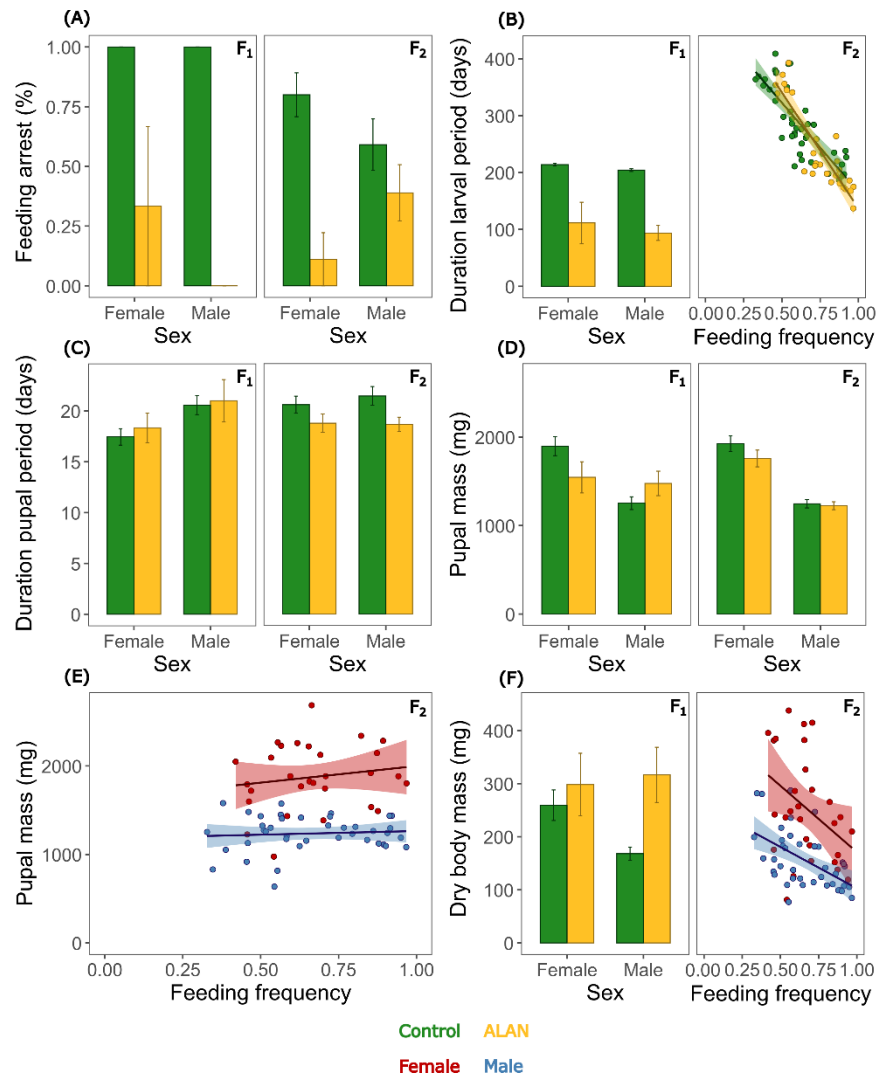


Fig. 2.2. (A-D,F) Raw mean values $\pm$ SE feeding arrest, duration of the larval and pupal stage, pupal mass and dry body mass in F₁ and F₂ generation female and male *Arctia caja* under the control and ALAN treatment. (B) Raw values and linear regression lines (and 95 % confidence intervals: shaded 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.

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 *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 (McLay *et al.*, 2018; Ayalon *et al.*, 2019; Grunst *et al.*, 2020), defined as a deviation from homeostasis. When stress builds up, it could eventually lead to elevated mortality rates (McLay *et al.*, 2017; O'Connor *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 (Bedrosian *et al.*, 2011; Adamo, 2017; Durrant *et al.*, 2020a). 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 F₁ generation compared to the F₂ generation. The F₂ generation is composed of the direct offspring of the surviving individuals of the F₁ generation. Therefore, some selection may already have taken place during the F₁ generation experiment due to lower survival of some genotypes and individuals killed by pathogens⁶ (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 (van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Merckx *et al.*, 2023). Here, we showed the same for caterpillars with a diurnal activity peak and larval hibernation. Diapause

⁶ Survival F₁: family MJ1 < MJ2 and R; F₂: no significant difference between origin mothers and fathers

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 & 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., Lamunyon, 1997; Heisswolf *et al.*, 2009; Garrad *et al.*, 2016). 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 (van Geffen *et al.*, 2014; Grenis & Murphy, 2019). 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 (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022), 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 F₁ 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 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 lx) 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: *Chapter 4*), 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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Appendix C2. Supplementary Information for 2. Artificial light at night reduces larval survival and constrains female body mass in a capital breeding moth

Authors: Evert Van de Schoot, Renate A. Wesselingh and Hans Van Dyck

Table S2.1. Minimum, maximum and raw mean values $\pm$ SE for the developmental variables in females and males under the control and ALAN treatment in the F₁ generation.

		Control			ALAN		
		Min	Max	Mean $\pm$ SE	Min	Max	Mean $\pm$ SE
Duration of larval period (days)	F	193	236	214 $\pm$ 2	69	184	111 $\pm$ 36
	M	192	225	204 $\pm$ 2	56	120	94 $\pm$ 13
Duration of pupal period (days)	F	13	26	17 $\pm$ 1	16	21	18 $\pm$ 1
	M	16	28	21 $\pm$ 1	15	25	20 $\pm$ 2
Pupal mass (mg)	F	889.54	2668.92	1898.74 $\pm$ 108.44	1211.08	1808.89	1545.29 $\pm$ 176.15
	M	794.83	1825.04	1253.20 $\pm$ 72.04	1081.21	1693.23	1476.21 $\pm$ 138.12
Dry body mass (mg)	F	57.04	496.31	259.34 $\pm$ 28.75	188.76	390.31	298.34 $\pm$ 58.84
	M	77.16	219.91	168.08 $\pm$ 12.35	246.04	418.08	316.52 $\pm$ 52.04

Table S2.2. Minimum, maximum and raw mean values $\pm$ SE for the developmental variables in females and males under the control and ALAN treatment in the F₂ generation.

		Control			ALAN		
		Min	Max	Mean $\pm$ SE	Min	Max	Mean $\pm$ SE
Feeding frequency	F	0.420	0.893	0.611 $\pm$ 0.028	0.469	0.968	0.799 $\pm$ 0.051
	M	0.328	0.921	0.615 $\pm$ 0.042	0.459	0.967	0.720 $\pm$ 0.040
Duration of larval period (days)	F	187	409	292 $\pm$ 13	175	339	220 $\pm$ 18
	M	194	392	282 $\pm$ 15	137	393	251 $\pm$ 20
Duration of pupal period (days)	F	14	28	21 $\pm$ 1	15	24	19 $\pm$ 1
	M	16	31	21 $\pm$ 1	11	22	19 $\pm$ 1
Pupal mass (mg)	F	975.30	2685.90	1927.65 $\pm$ 89.68	1384.96	2340.57	1758.07 $\pm$ 94.71
	M	815.46	1579.61	1245.96 $\pm$ 46.16	636.16	1463.68	1224.49 $\pm$ 44.85
Dry body mass (mg)	F	81.22	437.77	269.42 $\pm$ 23.76	119.08	384.57	218.24 $\pm$ 27.91
	M	76.93	287.33	159.09 $\pm$ 12.83	84.61	246.72	151.06 $\pm$ 11.69

Table S2.3. Sample sizes for each trait per generation, treatment and sex.

	F ₁ generation				F ₂ generation			
	Control		ALAN		Control		ALAN	
	F	M	F	M	F	M	F	M
Mortality	63		63		98		98	
Occurrence of feeding arrest	21	14	3	4	20	22	9	18
Feeding frequency	NA	NA	NA	NA	20	22	9	18
Duration of larval period	21	14	3	4	20	22	9	18
Duration of pupal period	20	14	3	3	20	22	9	18
Pupal mass	21	14	3	4	20	22	9	18
Dry body mass	19	13	3	3	20	22	9	18

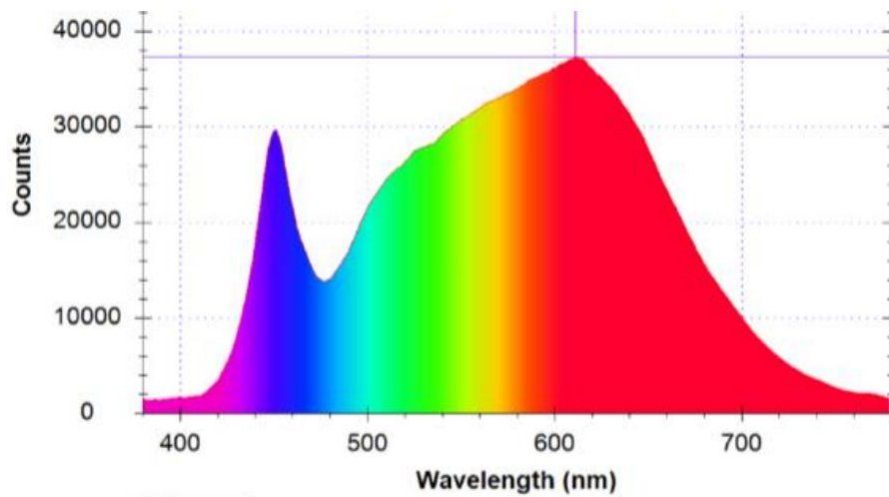


Fig. S2.1. Spectral composition of the diurnal light (VEGELED LO250 floodlight, Colasse). Data from www.colasse.be.

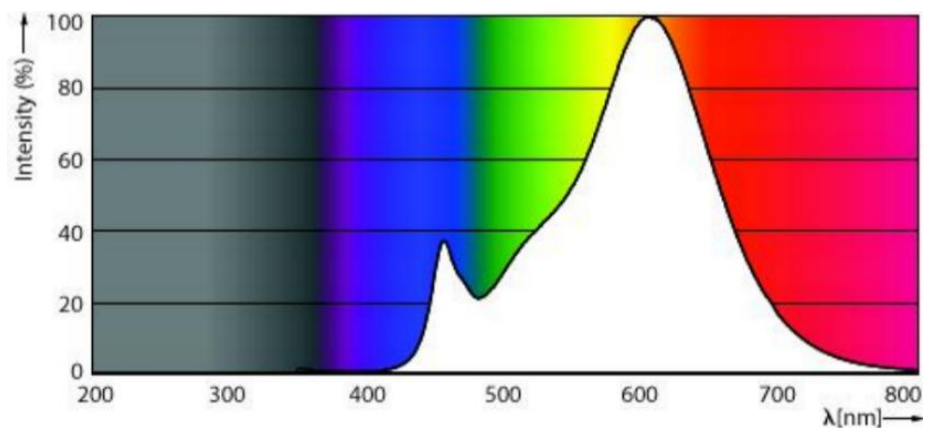


Fig. S2.2. Spectral composition of the ALAN light (Philips 1.4 W, 2700 K). Data from www.lighting.philips.be.

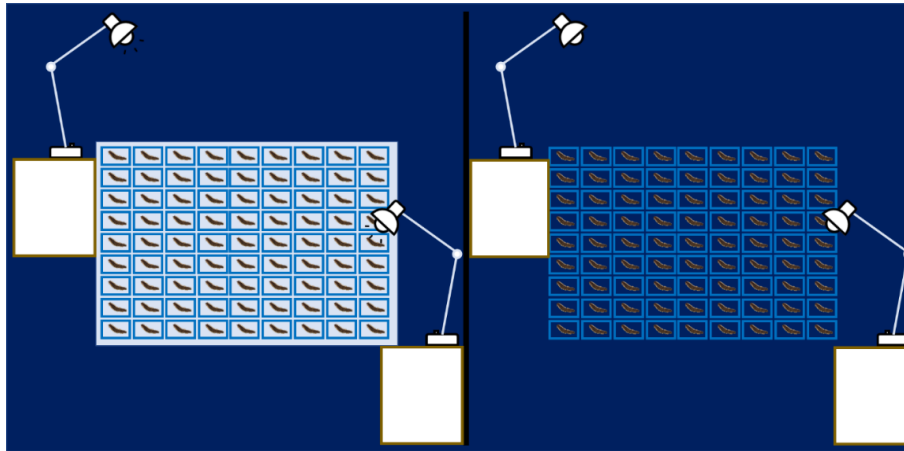


Fig. S2.3. Schematic overview of the experimental set-up for the F_1 generation. Left: the ALAN treatment (lightblue) receiving light from two lamps standing on a box (white rectangle); right: the control treatment. Both treatments were separated by a wall (black line), and switched sides after each feeding.

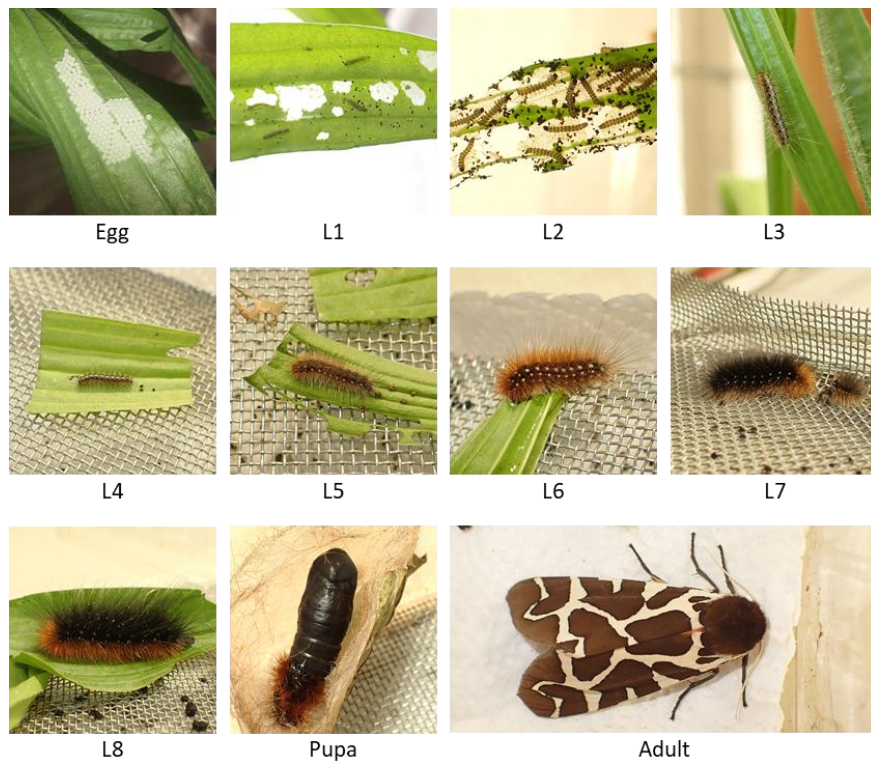


Fig. S2.4. Developmental stages of *A. caja* with the larval instars distinguished as in the F_1 generation experiment.

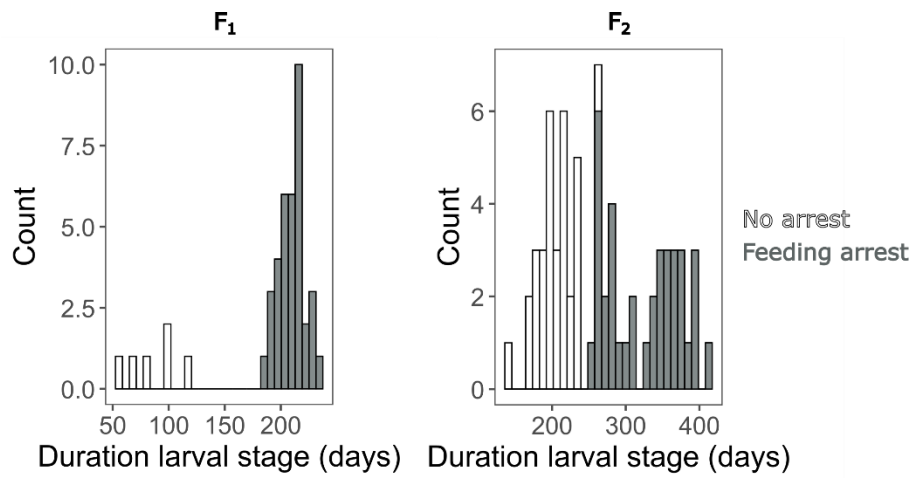


Fig. S2.5. Histograms of larval stage duration in the F_1 and F_2 generation, showing the thresholds for feeding arrest.

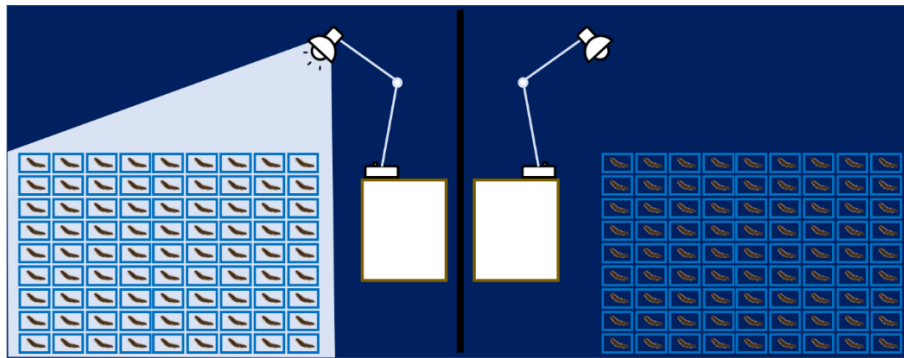


Fig. S2.6. Schematic overview of the experimental set-up for the F_1 generation. Left: the ALAN treatment (lightblue) receiving light from one lamp standing on a box (white rectangle); right: the control treatment. Both treatments were separated by a wall (black line), and switched sides after each feeding.

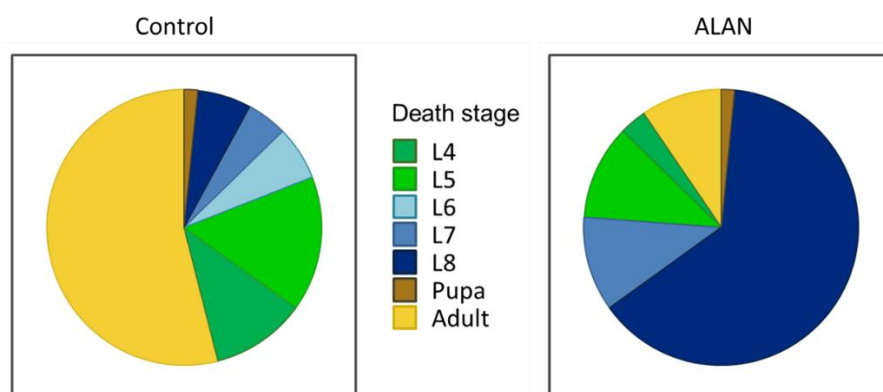


Fig. S2.7. Developmental stage at which the individuals in the F₁ generation experiment died.

CHAPTER 3

Experimental study on the impact of continuous and dynamic artificial light at night on moths originating from different skyglow conditions

Authors: Evert Van de Schoot, Marine Lonnoy, Ludovic Laroy, Renate A. Wesselingh and Hans Van Dyck

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In this chapter, we investigate the so far unaddressed impact of dynamic ALAN *versus* continuous ALAN on larval development and final body mass in two noctuid moths. Further, we explore potential adaptive responses in populations under higher skyglow conditions.

Abstract

Biodiversity is negatively affected by light pollution, caused by artificial light at night (ALAN). Light-emitting diodes facilitate new lighting technologies to mediate the negative effects of ALAN, such as dynamic ALAN where light intensity can be adjusted to traffic density. Organisms living in highly light-polluted areas may show adaptations to mitigate the negative effects of ALAN. In a split-brood rearing experiment, larvae of two moth species (*Ochropleura plecta* and *Agrotis exclamationis*) originating from low-medium and high-medium skyglow populations were grown under either continuous ALAN, dynamic ALAN or control-dark conditions. We tested for ALAN effects on larval mortality, feeding behaviour, development and body mass, and whether effects depended on skyglow levels in the population of origin. Contrary to previous studies, we found either no or positive effects of ALAN on larval development, with similar or stronger effects of dynamic ALAN compared to continuous ALAN. For *A. exclamationis*, we showed evidence for faster development, increased growth rate and higher body mass under ALAN. This could reduce larval exposure to parasites and increase fecundity. We found no evidence for evolutionary responses in low-medium or high-medium skyglow larvae. Our results show that ALAN does not affect larval development the same way in all species.

Introduction

Mankind is increasingly illuminating the nocturnal landscape by introducing artificial lighting at night (ALAN) in the environment, mainly in the form of public lighting (Kyba *et al.*, 2017). The light pollution this causes is not limited to the direct vicinity of the light, but is also reflected by the atmosphere and clouds, creating skyglow (Falchi *et al.*, 2016). Skyglow is much weaker in intensity than direct light pollution, but causes ALAN to spread up to several kilometres from its source in a cumulative way based on local clusters of lights.

The mounting evidence on negative effects of ALAN on biodiversity (Falcón *et al.*, 2020; Sanders *et al.*, 2021) combined with high costs of public lighting has prompted the question whether and how the use of ALAN can be better regulated (Challéat *et al.*, 2021; Morgan-Taylor, 2023). Limitations in the legal framework make it difficult to obtain a common policy on ALAN regulation. For example, the European policy framework requires that there is evidence of negative ALAN effects on populations of protected species (i.e., species on the Annexes of the Habitat and Birds Directive) or that the party

responsible for the ALAN emission causes intentional harm to organisms, which is often hard to prove (Schroer *et al.*, 2020). Some countries have developed binding laws, while others stick to non-binding guidelines for reducing light pollution (Widmer *et al.*, 2022). From a biodiversity perspective, policy strategies for darkening areas surrounding nature reserves (Guetté *et al.*, 2018; Peregrym *et al.*, 2020) and creating dark corridors (Zeale *et al.*, 2018; Sordello *et al.*, 2022) are increasingly proposed and defended. However, such ALAN mitigation measures are typically not isolated from politically difficult trade-offs with social and economic factors or arguments, of which safety (or at least safety perception) is usually considered the most important (Morgan-Taylor, 2023). The transition from classic light sources (e.g., sodium) to light emitting diodes (LED) led to an increase of short-wavelength light, potentially increasing damage to biodiversity (Gaston & Sánchez de Miguel, 2022). However, it has also stimulated higher flexibility of ALAN regulation (Challéat *et al.*, 2021). In places where the traffic volume is limited but lighting remains necessary, two main types of mitigation measures have been adopted. First, the light spectrum can be changed towards longer wavelengths like amber or red light (e.g., Deichmann *et al.*, 2021). This so-called ‘bat-friendly’ light has the purpose to reduce attractive or repulsive effects of streetlights to flying insects and thus bats (Spoelstra *et al.*, 2015). Secondly, there are dynamic streetlights whose intensity can be adjusted according to the operational need for illumination depending on the amount or presence of traffic or passers-by. So-called ‘smart streetlights’ are an example. These streetlights have a motion detection system that only switches on when a person or vehicle passes and switches off again after a fixed, typically short, period of illumination. This should significantly reduce exposure time to ALAN. However, a recent study showed that even a short exposure to ALAN can cause behavioural changes in adult moths (Fabusova *et al.*, 2024). To what extent the ecological effects of dynamic ALAN differ from continuous ALAN is still poorly understood.

Here we experimentally tested the impact of both types of ALAN on the growth and larval development of moths. Moths are an emblematic species group when it comes to light pollution, since most species are nocturnal and show a typical flight-to-light response (van Langevelde *et al.*, 2018; Fabian *et al.*, 2024). ALAN does not only cause direct behavioural effects in adult moths, but may also affect larval development. Previous studies have mainly shown negative effects of ALAN on larval development, including increased larval mortality (Van de Schoot *et al.*, 2025c: *Chapter 2*), diapause inhibition (van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*), faster development (van Geffen *et al.*, 2014; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*) and reduced

growth rate (Grenis & Murphy, 2019). Eventually, ontogenetic exposure to ALAN may lead to a reduction in adult body size (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025c: *Chapter 2*), which in turn may have negative effects on fecundity, particularly in females (Lamunyon, 1997; Heisswolf *et al.*, 2009), and on mobility (e.g., Berwaerts *et al.*, 2002).

When exposure to ALAN is accompanied by fitness costs in inherited traits for a significant part of a population, it has the potential to drive evolutionary responses (Hopkins *et al.*, 2018). Altermatt and Ebert (2016) showed that ermine moths originating from urban, light-polluted areas had a weaker flight-to-light response compared to conspecifics of rural, dark areas, suggesting an adaptive response against the negative effects of flight-to-light. It was recently shown that these differences related to changes in wing morphology (Van de Schoot *et al.*, 2024: *Chapter 4*). For intraspecific variation in adult feeding and mate calling behaviour no such adaptive responses have been found, even though both traits were negatively affected by ALAN (Cieraad *et al.*, 2022). Similar studies on adaptative potential relative to larval development are currently lacking. These previous studies collected moths close to streetlights (Altermatt & Ebert, 2016; Cieraad *et al.*, 2022). For species where the majority of adults are assumed to stay close to the host plant on which they grew up as larvae, like in the case of ermine moths (Menken *et al.*, 1992), this can indeed be useful. However, for species that show higher mobility, it is likely that the general density of public lighting at the landscape scale, which is reflected in the skyglow level, is a more important driver of evolutionary processes than individual light sources. Merckx *et al.* (2023) showed ALAN at skyglow intensity is sufficient to constrain larval growth and inhibit diapause induction in *Chiasmia clathrata*. Therefore, chronic exposure to high skyglow levels has the potential to drive adaptive responses that could enhance larval development under ALAN.

In this study, we tested for differences in the impact of ALAN on larval development of moths whose mother originated from either high-medium or low-medium skyglow areas, allowing to examine both local adaptation and plastic constraints. In a split-brood breeding experiment, larvae originating from populations under high-medium and low-medium skyglow levels were reared under either continuous ALAN, dynamic ALAN or dark night conditions. We tested the treatments in two generalist moth species, *Ochropleura plecta* and *Agrotis exclamationis* (Noctuidae), which are both still common so they are an interesting complement to previous studies that used more specialised or less common study species (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*). Moreover, this choice allowed us to sample females in reasonable numbers and well distributed over our study regions. Noctuidae are

particularly attracted to short-wavelength ALAN, which is relevant given the current shift towards LED streetlights that usually emit more short-wavelength light. Previous studies of ALAN on larval survival found either no effect (Grenis & Murphy, 2019; Merckx *et al.*, 2023) or negative effects (Van de Schoot *et al.*, 2025c: *Chapter 2*). ALAN exposure usually accelerates larval development, either through diapause inhibition (Van de Schoot *et al.*, 2025c: *Chapter 2*), but also independently of such a diapause inhibition (van Geffen *et al.*, 2014; Merckx *et al.*, 2023). When the impact is not compensated by a higher growth rate, it leads to reduced final body mass, as shown in previous studies (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025c: *Chapter 2*). Dynamic ALAN significantly reduces the exposure time compared to continuous ALAN and can therefore be expected to have a weaker effect on larval development. If an adaptive response is present in high-medium skyglow larvae, we predict higher larval survival, growth rate and final body mass under ALAN conditions compared to low-medium skyglow larvae.

Material and Methods

Study species

For our experimental study, we selected two noctuid species: the heart and dart *Agrotis exclamationis* L. and the flame shoulder *Ochropleura plecta* L. (Lepidoptera: Noctuidae). Adults of both species drink nectar (Waring *et al.*, 2015) and can be considered as, at least to a significant extent, income breeders (Tammaru & Haukioja, 1996). *Agrotis exclamationis* is a common and widespread species in the temperate and Mediterranean areas of the Palearctic region (GBIF.org. <https://www.gbif.org/>). It is present in several kinds of open habitats, including agricultural areas, and flies in two generations a year (from May to October in Belgium: Waring *et al.*, 2015). The larvae are nocturnal and, during the day, they hide in litter or soil. They are able to feed on a wide range of herbaceous plants and grasses, including crops. In autumn, full-grown larvae make a cocoon in the soil to hibernate.

Ochropleura plecta is a Holarctic moth species that is common and widespread in the temperate and subpolar zones, but rarer in the Mediterranean zone (GBIF.org. <https://www.gbif.org/>). It is characterised as a habitat generalist, being present in both open habitats and woodlands. It has two to three generations a year (from April to October in Belgium: Waring *et al.*, 2015). Larvae feed on a large variety of herbaceous plants

during the night and hide on the food plant during the day. They hibernate as pupae in the soil.

Female sampling and pre-experimental breeding conditions

Females were sampled in two regions in Belgium that differ significantly in skyglow (Fig. S3.1, Appendix C3); Central Belgium with relatively high-medium skyglow levels (SQM: 19.50–20.43 mag./arc sec², sky brightness: 727–1711 $\mu\text{cd}/\text{m}^2$) and Southern Belgium with relatively low-medium skyglow levels (SQM 20.82–21.30 mag./arc sec², sky brightness: 326–507 $\mu\text{cd}/\text{m}^2$) (data from <http://www.lightpollutionmap.info>; Falchi *et al.*, 2016). They were captured with a Skinner light trap with a mercury vapour lamp and LedTraps with a 5050 UV LED strip (van Deijk *et al.*, 2024) from the end of May to the beginning of July 2023. Females were transferred to the lab and kept in plastic boxes (115 x 115 x 60 mm)⁷ with 1-mm holes for aeration, a 1.5-mL tube with 10 % honey-water solution and paper towel for oviposition. For *A. exclamatoris*, eggs from 23 females were obtained (11 families from the high-medium skyglow region, 12 from the low-medium skyglow region). For *O. plecta*, eggs from 12 females were obtained (6 families from each region). We did not test for genetic relatedness between the females originating from the same sampling site, but both species are common, widespread species of reasonable mobility; hence, the probability of having caught related females is assumed to be low. Eggs and resulting larvae were reared in groups of c. 10 larvae/box in a climate chamber under a day-night cycle of LD 16:8 and at a day and night temperature of 23 °C and 18 °C, respectively. Larvae were fed a mixture of *Plantago lanceolata* and *Taraxacum officinale* leaves until the start of the experiment.

Split-brood breeding experiment

For each family of *A. exclamatoris* and *O. plecta*, 6 to 12 and 6 to 24 larvae, respectively, were transferred to individual boxes with aeration holes and paper towel in a climate room under a day-night cycle of LD 16:8 and at a day and night temperature of 23 °C and 18 °C with measured mean temperatures in the rearing boxes reaching 24.3 °C and 19.9 °C. The larvae were equally divided over two climate rooms with each three light treatments; (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 lx); the time scheme was programmed on Raspberry Pi Zero W (Raspberry Pi

⁷ Biopack

Foundation) and is shown in Table S3.1 (Appendix C3); (iii) control treatment with dark nights (0.03–0.16 lx). Every day, the larvae were checked for moulting and were fed with fresh pieces of wild-picked *P. lanceolata* leaves. The size of a single piece of food plant was fixed and the number of pieces was adjusted to the amount eaten during the previous day. A plant mister was used to increase relative humidity (above 75 %). Paper towel was replaced and faeces removed regularly. Larvae were weighed with a microbalance (Mettler MT5 microbalance; precision $\pm 10^{-5}$ g) at the beginning of the experiment and then every 5 or 7 days for *A. exclamatoris* and *O. plecta*, respectively. Full-grown larvae moulted to a pre-pupal stage in which they usually construct a cocoon underneath the paper towel where they pupate. Pupae were weighed four days after pupation and adults were weighed on the day of eclosion. Mass loss upon eclosion was determined as $(1 - \text{adult mass/pupal mass}) \cdot 100$ (Molleman *et al.*, 2011). Growth rate was only calculated for *A. exclamatoris*, since *O. plecta* had a very short development time. Overall exponential growth rate for *A. exclamatoris* was calculated as $(\text{maximal larval mass}/\text{larval mass at start experiment})^{(1/\text{day of maximal larval mass})} - 1$. Initial growth rate was calculated in the same way for the first 10 days of the experiment and final growth rate for the last 10 days before maximal larval mass was reached. Adults were provided with a tube of honey-water solution for five days, after which they were stored in the freezer (–21 °C). After daily handling, the position of the rearing boxes was randomized.

Statistical analysis

First, we tested for differences in survival, larval development, feeding behaviour and body mass between *O. plecta* and *A. exclamatoris*, after which we tested for the effects of ALAN treatment, skyglow origin and sex as well as their two-way interactions, on these factors for both species separately. Non-significant two-way interactions were removed from the models. Differences in mortality were tested using generalized linear mixed models (GLMM) with a binomial error distribution. GLMMs with a Poisson error distribution were used to test for differences in duration of the larval and pupal period. Larval body mass at the start of the experiment was included as a covariate for duration of the larval period. Feeding frequency was tested using a GLMM with a binomial error distribution and the amount of eaten food was tested using a GLMM with a gamma error distribution. Differences in body mass and mass loss upon eclosion were tested using linear mixed models (LMM). Duration of the larval period and the interaction effects with ALAN treatment, skyglow origin and sex were also included to test for differences in body mass and feeding behaviour. LMMs were used to

test for differences in exponential growth rate in *A. exclamatoris*. In all LMM and GLMM models, climate room was included as a covariate and family nested within sampling site was included as a random factor. In case there was a significant treatment effect, a post-hoc test with Benjamini-Hochberg correction was performed to compare the different treatments. Sample sizes are provided in Tables S3.2 and S3.3 (Appendix C3). All analyses were performed in R 4.4.2 (R Development Core Team, R Foundation for Statistical Computing, Austria. <http://www.R-project.org/>). We reported our results in line with the good practice of the language of evidence (Muff *et al.*, 2022).

Results

Except for larval survival, we found moderate to very strong evidence for differences in all developmental variables and body mass between *O. plecta* and *A. exclamatoris* (Table S3.4, Appendix C3). Therefore, further analyses were performed for both species separately as to avoid collinearity effects between species identity and developmental or body mass traits.

Ochroleuca plecta

Development and feeding behaviour

The ALAN treatments had no effect on larval survival of *O. plecta* and also the skyglow level at the population of origin had no significant effect on larval survival (Table 3.1). The duration of the larval period was not affected by ALAN treatment, skyglow level at the population of origin or sex, but larvae of lower mass at the start of the experiment showed a longer development time (very strong evidence; Table 3.1). We found moderate evidence for higher feeding frequency in males than in females. The difference between the sexes was only significant under dynamic ALAN ($t = 2.94$, $P = 0.004$; Fig. 3.1a, Table 3.1). Female larvae ate more than male larvae (weak evidence; Fig. 3.1b) and the amount of food eaten was positively related to the duration of the larval period (very strong evidence; Table 3.1).

Body mass

Maximal larval mass was not affected by ALAN treatment, skyglow level at the population of origin, sex or duration of the larval period (Table 3.1). Pupal mass tended to be higher under continuous ($t = 2.43$, $P = 0.050$) and dynamic ALAN ($t = 1.94$, $P = 0.081$) than under the control treatment (Fig. 3.1c). We

also found strong evidence for a positive relationship between pupal mass and duration of the larval period (Table 3.1). Mass loss at eclosion was higher in males than in females (very strong evidence; Fig. 3.1d) leading to a higher adult body mass in females than in males (very strong evidence; Fig. 3.1e), which tended to increase with duration of the larval period (weak evidence; Table 3.1).

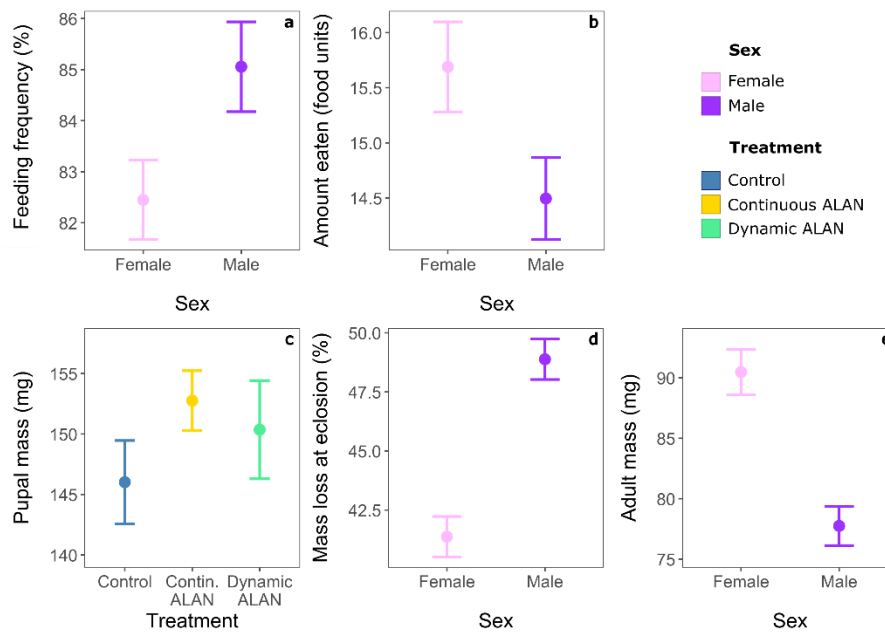


Fig. 3.1. (a,b,d,e) Raw mean values $\pm$ SE of feeding frequency, amount eaten, mass loss at eclosion and adult mass in female and male *Ochropleura plecta*. (c) Raw mean values $\pm$ SE of pupal mass under the ALAN treatments.

Table 3.1. Statistical output for differences in larval survival and development for *Ochropleura plecta* and *Agrotis exclamationis*. All tests are based on d.f. = 1, except for ALAN-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.

	<i>O. plecta</i>	χ^2	P	<i>A. exclamationis</i>	χ^2	P
Larval survival	Treatment	1.03	0.598	Treatment	0.84	0.656
	Skyglow	0.24	0.624	Skyglow	1.75	0.186
	Room	0.83	0.361	Room	4.24	0.039
Duration of larval period	Treatment	0.31	0.856	Treatment	26.49	< 0.001
	Skyglow	0.24	0.627	Skyglow	1.39	0.239
	Sex	0.99	0.320	Sex	6.46	0.011
	Larval mass at start	29.44	< 0.001	Larval mass at start	27.93	< 0.001
	Room	0.00	0.968	Room	17.32	< 0.001
				Skyglow x Sex	13.39	< 0.001
Feeding frequency	Treatment	4.45	0.108	Treatment	4.05	0.132
	Skyglow	0.26	0.609	Skyglow	0.00	0.960
	Sex	5.79	0.016	Sex	0.52	0.473
	Duration of larval period	0.87	0.350	Duration of larval period	3.94	0.047
	Room	3.22	0.073°	Room	2.67	0.102
				Treatment x duration of larval period	5.54	0.063°
Amount eaten	Treatment	1.28	0.528	Treatment	3.07	0.216
	Skyglow	0.64	0.424	Skyglow	2.64	0.104
	Sex	2.73	0.098°	Sex	0.65	0.420
	Duration of larval period	84.52	< 0.001	Duration of larval period	200.74	< 0.001
	Room	2.56	0.110	Room	0.19	0.667
Maximal larval mass	Treatment	4.52	0.104	Treatment	7.12	0.029
	Skyglow	0.32	0.571	Skyglow	0.194	0.659
	Sex	0.80	0.370	Sex	0.00	0.981
	Duration of larval period	1.37	0.241	Duration of larval period	29.68	< 0.001
	Room	1.32	0.250	Room	3.05	0.081°
Pupal mass	Treatment	6.75	0.034	Treatment	16.58	< 0.001
	Skyglow	1.12	0.290	Skyglow	0.22	0.638
	Sex	0.03	0.872	Sex	3.21	0.073°
	Duration of larval period	7.88	0.005	Duration of larval period	57.78	< 0.001
	Room	0.39	0.534	Room	2.09	0.148
				Treatment x Sex	8.71	0.013

Table 3.1. Continued

	<i>O. plecta</i>	χ^2	P	<i>A. exclamationis</i>	χ^2	P
Adult mass	Treatment	3.77	0.152	Treatment	12.42	0.002
	Skyglow	0.96	0.327	Skyglow	0.33	0.565
	Sex	23.72	< 0.001	Sex	23.21	< 0.001
	Duration of larval period	3.19	0.074°	Duration of larval period	47.14	< 0.001
	Room	0.81	0.368	Room	5.60	0.018
Mass loss at eclosion	Treatment	2.60	0.272	Treatment	5.34	0.069°
	Skyglow	0.44	0.508	Skyglow	0.40	0.527
	Sex	39.30	< 0.001	Sex	72.80	< 0.001
	Room	0.10	0.747	Room	0.31	0.578

*Agrotis exclamationis**Development and feeding behaviour*

Larval survival was not affected by ALAN treatment or skyglow at the population of origin (Table 3.1). Larvae under dynamic ALAN developed faster than larvae in the control treatment ($t = 5.04$, $P < 0.001$) and continuous ALAN ($t = 3.33$, $P = 0.003$; Fig. 3.2a). Larvae originating from high-medium skyglow populations developed faster than larvae from low-medium skyglow populations and this difference was stronger in males than in females (strong evidence; Fig. 3.2b, Table 3.1). Larvae of lower mass at the start of the experiment showed a longer larval development time (Table 3.1). Feeding frequency decreased with duration of the larval period and this effect was stronger under continuous ALAN (moderate evidence; Fig. 3.2c). The amount of food eaten was positively related to duration of the larval period (very strong evidence; Table 3.1).

Body mass

Maximal larval mass was higher under dynamic ALAN than under the control treatment ($t = 2.56$, $P = 0.031$; Fig. 3.2d) and increased with duration of the larval period (very strong evidence; Table 3.1). While pupal mass tended to be higher for males than females under the control treatment ($t = 1.78$, $P = 0.077$) and continuous ALAN ($t = 1.94$, $P = 0.055$), the opposite was found under dynamic ALAN ($t = -1.72$, $P = 0.087$; Fig. 3.2e). Pupal mass also increased with duration of the larval period (very strong evidence; Table 3.1). Mass loss at eclosion tended to be lower under continuous ALAN than under

the control treatment ($t = 2.26$, $P = 0.065$) and was higher in males than in females (very strong evidence; Fig. 3.2f). Adult body mass was higher under continuous ($t = 3.32$, $P = 0.003$) and dynamic ALAN ($t = 2.60$, $P = 0.016$) than under the control treatment, higher in females than in males (very strong evidence; Fig. 3.2g) and increased with the duration of the larval period (very strong evidence; Table 3.1).

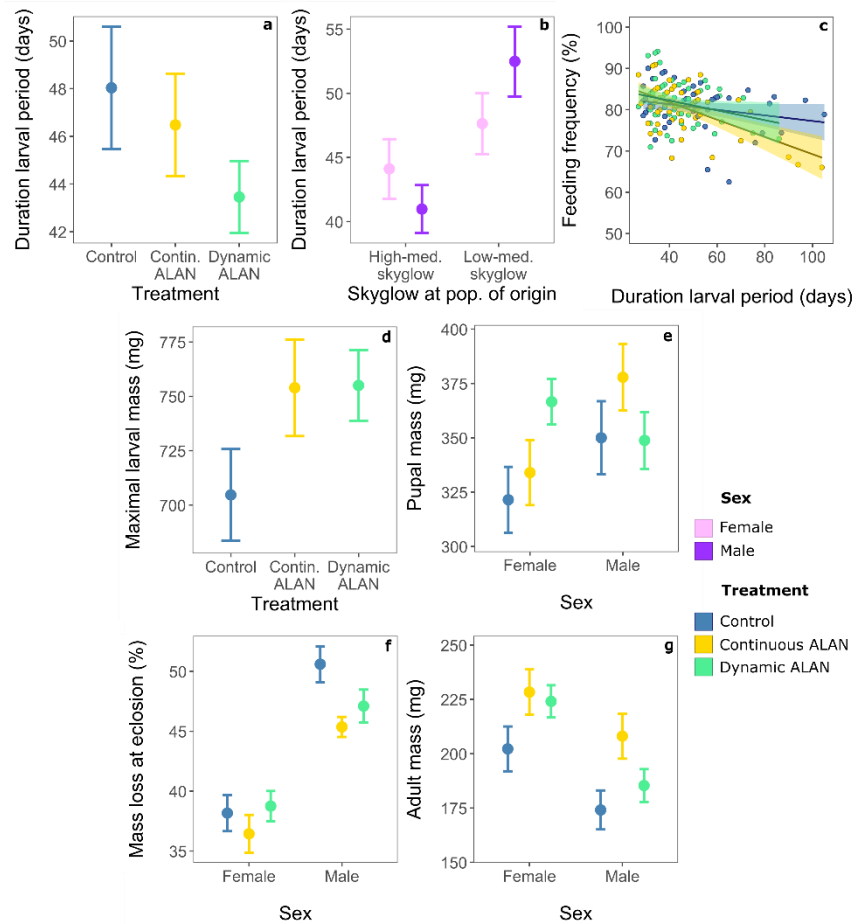


Fig. 3.2. (a,d) Raw mean values $\pm$ SE of duration of the larval period and maximal larval mass in *Agrotis exclamationis* under the ALAN treatments. (b) Raw mean values $\pm$ SE of duration of the larval period in females and males originating from high-medium and low-medium skygglow populations. (c) Raw values and linear regression lines (and 95 % confidence intervals: shaded area) of feeding frequency in function of duration of the larval period under the ALAN treatments. (e-g) Raw mean values $\pm$ SE of pupal mass, mass loss at eclosion and adult mass in females and males under the ALAN treatments.

Larval growth rate in *A. exclamationis*

We found moderate evidence for higher overall growth rate under dynamic ALAN than under the control treatment ($t = 2.48$, $P = 0.043$; Fig. 3.3a). This tended to be the case for initial growth rate ($t = 2.29$, $P = 0.061$; Fig. 3.3c) rather than growth rate at the end of the larval period ($t = 0.87$, $P = 0.663$; Table 3.2). We found strong evidence for higher initial growth rate in males than in females (Fig. 3.3d, Table 3.2). For overall growth rate, no sex difference was found for larvae originating from high-medium skyglow populations, but males had a lower growth rate than females when originating from low-medium skyglow populations (moderate evidence; Fig. 3.3b, Table 3.2). Growth rate at the end of the larval period was not affected by ALAN treatment, skyglow level at the population of origin or sex (Table 3.2).

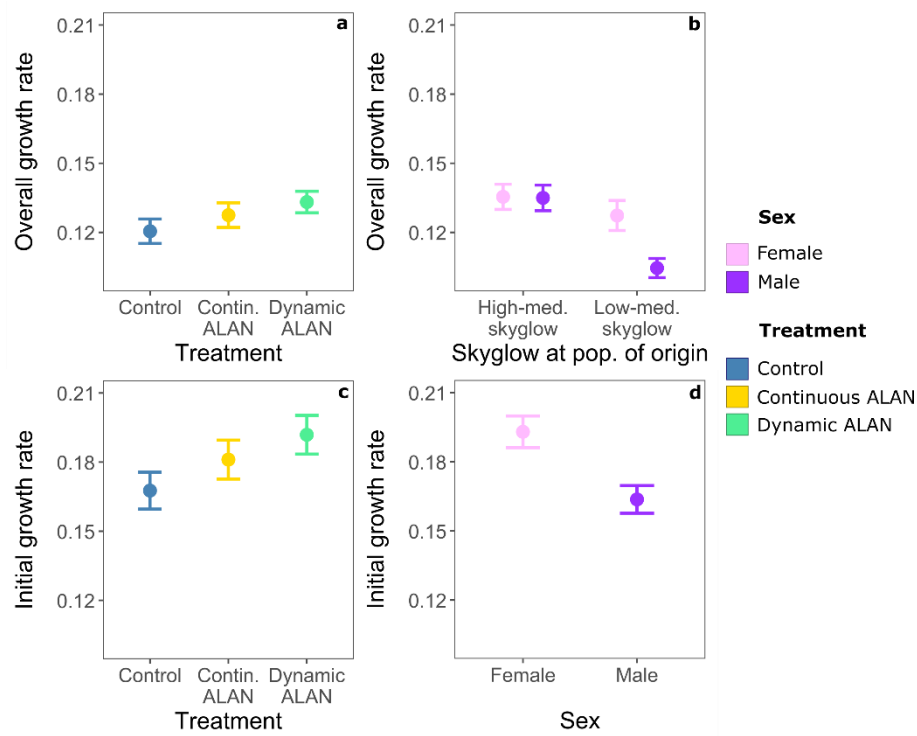


Fig. 3.3. (a,c) Raw mean values $\pm$ SE of overall and initial exponential growth rate in *Agrotis exclamationis* under the ALAN treatments. (b) Raw mean values $\pm$ SE of overall growth rate in females and males originating from high-medium and low-medium skyglow populations. (d) Raw mean values $\pm$ SE of initial growth rate in females and males.

Table 3.2. Statistical output for differences in exponential growth rate for *Agrotis exclamationis*. 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.

	<i>A. exclamationis</i>	χ^2	P
Exponential growth rate (overall)	Treatment	6.23	0.044
	Skyglow	0.90	0.342
	Sex	0.01	0.909
	Room	7.86	0.005
	Skyglow x Sex	4.42	0.035
Exponential growth rate (initial)	Treatment	5.31	0.070°
	Skyglow	1.80	0.179
	Sex	8.81	0.003
	Room	1.35	0.246
Exponential growth rate (final)	Treatment	1.12	0.572
	Skyglow	0.57	0.450
	Sex	0.34	0.562
	Room	0.61	0.433

Discussion

In this study, we investigated whether larval growth and development in two noctuid moths were affected by continuous and dynamic ALAN and whether ALAN effects varied between populations with different skyglow levels. For *A. exclamationis*, our results show evidence for faster larval development and higher growth rate under dynamic ALAN and increased body mass under both types of ALAN. For *O. plecta*, only pupal mass tended to increase under ALAN. The observed differences were mainly sex-related, while the skyglow level of the population of origin had hardly any effect on larval development. We discuss the implications of our results for the studied species and how they relate to previous studies, how the effects of dynamic ALAN compare to continuous ALAN, the lack of effects of skyglow levels at the population of origin, and we consider the extent to which our results can be extrapolated to other moth species.

For larvae, it is often advantageous to have a shorter development time, since this reduces the risk of parasitism (Benrey & Denno, 1997; Chen & Chen, 2018) and provides competitive advantages when food sources are limited (Rowe & Ludwig, 1991; Manthey *et al.*, 2024). When this is coupled with increased body mass, as we found for *A. exclamationis*, it can also have benefits for fecundity (Lamunyon, 1997; Heisswolf *et al.*, 2009) and mobility (Merckx *et al.*, 2018). In contrast to previous studies in moths, where fast

larval development was often coupled with lower body mass (van Geffen *et al.*, 2014; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*), we found no to even positive effects of ALAN on larval development. Recent studies on moth communities indeed show that most species are negatively affected by light pollution, however, there are also species that show positive correlations with ALAN (Grenis *et al.*, 2023; Van de Schoot *et al.*, 2025b: *Chapter 6*). This suggests that not all species respond in the same way to light pollution. For example, studies in other insect groups have shown no to positive effects of ALAN on juvenile development (Durrant *et al.*, 2018; McLay *et al.*, 2018; Owens & Lewis, 2021), although negative effects may still be present at the physiological level and in other life stages (McLay *et al.*, 2018; Durrant *et al.*, 2020b; Owens & Lewis, 2021).

Growth rate is one of the important factors determining larval development time and body mass (Davidowitz & Nijhout, 2004). We show evidence for increased growth rate under dynamic ALAN. It seems that this difference was mainly observable at the beginning of the experimental treatment, although the evidence for this is rather weak. Previous studies have shown that ALAN effects on growth rate can already occur soon after the start of exposure (Luarte *et al.*, 2016a; Grenis & Murphy, 2019). Later in development, differences in growth rate were no longer significant, but these were possibly masked by interindividual variation in development time.

Our dynamic ALAN treatment reduced the exposure time by two-thirds compared to the continuous ALAN treatment and was therefore expected to have a weaker effect on larval development (as previously demonstrated for flight-to-light: Bolliger *et al.*, 2020). Yet dynamic ALAN affected the duration of the larval period, growth rate and maximal larval mass more strongly than continuous ALAN. Moreover, both ALAN conditions showed similar effects on adult body mass. These results indicate that dynamic ALAN can at least have as strong effects as continuous ALAN, which is in line with a previous study that showed stronger negative effects of part-night exposure to ALAN on aphid colonies compared to full-night ALAN (Heinen *et al.*, 2023). If this would also be the case in species negatively affected by ALAN, it would mean that dynamic streetlights are not necessarily better for moths (Owens *et al.*, 2024), at least when it comes to larval development, but this remains to be tested.

An evolutionary response in larval development under ALAN would require negative or positive fitness consequences (Hopkins *et al.*, 2018). For *O. plecta*, we found no or only slightly positive ALAN effects and, consequently, there was a lack of adaptive response in this species. On the other hand, our results suggest positive effects of ALAN in *A. exclamationis*. However, also for this species, we did not show evidence for an adaptive

response in moths originating from high-medium skyglow populations. We found barely any evidence for effects of skyglow levels at the population of origin *per se*. Possibly, populations from high-medium and low-medium skyglow areas may be genetically more strongly connected to each other than we assumed. In fact, our low-medium skyglow populations were only 15–35 km away from areas with high-medium skyglow levels. For good flying species like *A. exclamatoris*, and to a somewhat lesser extent *O. plecta* (Jones *et al.*, 2016), these distances are certainly passable. It is therefore not inconceivable that gene flow between these populations occurs to a greater or lesser extent. It would therefore be interesting to compare the responses of different populations in combination with population genetic work (e.g., González-Castellano *et al.*, 2023), but local adaptation can also be maintained despite gene flow (Tigano & Friesen, 2016). Moreover, our study area (i.e., Belgium) did not allow to select sampling sites with actual zero or low skyglow levels (Falchi *et al.*, 2016). Finally, it should be noted that, although we selected sites without significant local differences in urbanisation levels, we could not fully control for other potentially confounding factors that differ between our sampled regions (*cf.* Grenis *et al.*, 2023; Ghosh *et al.*, 2024) like altitude, temperature and vegetation. Future studies should therefore aim to disentangle the impact of these environmental variables as much as possible by including several regional replicates, which would require a much larger research effort (Sanetra *et al.*, 2024).

The more hidden lifestyle of *A. exclamatoris* caterpillars may limit both potential harmful and positive effects of ALAN, while *O. plecta* larvae are likely to experience higher exposure (Waring *et al.*, 2015; Summers *et al.*, 2024). Yet, while we showed evidence for multiple ALAN effects on larval development in *A. exclamatoris*, effects in *O. plecta* were mostly absent. However, body mass response to ALAN went in the same direction for both species, although non-significant for *O. plecta*. It should therefore be noted that for practical reasons, *O. plecta* larvae were exposed to the experimental treatments at a higher starting mass compared to *A. exclamatoris*. As a result, the experimental period was c. two to three times shorter for *O. plecta* than for *A. exclamatoris* which may have led to the lack of significant differences in the former species.

One of the ways ALAN potentially acts on moth ontogeny is by changing food consumption (Haynes *et al.*, 2023). For larvae that show a nocturnal activity peak, ALAN can be expected to disturb feeding, while diurnal larvae could in turn see their activity period extended. Our study species have larvae that are mainly nocturnal, but despite faster development under ALAN, they also had a higher body mass, suggesting that feeding behaviour also changes under ALAN. Larvae that developed faster had a higher feeding frequency,

although feeding frequency did not differ between ALAN treatments. However, we showed that faster-developing larvae in total consumed a lower quantity of food, yet it is possible that they consumed larger amounts per day or exhibited higher levels of energy efficiency, but this remains to be tested.

Depending on the ability to still take up nutrients during the adult stage, the body mass at the end of ontogeny determines to a greater or lesser extent the reproductive and dispersal capacity of the adult (Tammara & Haukioja, 1996). Adults are often very motile making them sometimes difficult to weigh, so it is often opted to measure maximal larval mass or pupal mass instead of adult mass (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023). Maximal larval mass is often a less precise measurement, because larvae are typically weighed only once or twice a week, which means the actual day of maximum mass can be missed. In turn, pupal mass is usually measured at a fixed number of days after pupation, making it a more precise and therefore a better proxy for adult mass. However, during the pupal period and adult eclosion, some body mass is also lost and this is usually more in males than in females (Molleman *et al.*, 2011). In our study, we see for maximal larval mass in *A. exclamatoris* that only dynamic ALAN leads to higher mass compared to the control treatment; for pupal mass, continuous ALAN also tends to lead to higher mass than the control treatment and male mass tends to be higher than in females. But under continuous ALAN, less mass was lost during eclosion which ultimately caused adult mass under continuous ALAN to be slightly higher than under dynamic ALAN. Moreover, males lost c. one-fourth more mass than females, resulting in higher adult mass in females compared to males. This indicates that conclusions should always be treated with some caution when using proxies for final body mass.

Our results suggest that exposure to ALAN during development has a rather positive effect on our study species, especially *A. exclamatoris*. However, in contrast to previous studies that mainly showed negative ALAN effects on larval development (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: Chapter 2), this study involves two highly generalist species that are still abundant in residential areas (Waring *et al.*, 2015). These species seem well adapted or adaptable to changes associated with urbanisation, but this is usually only true for a limited amount of insect species (Merckx & Van Dyck, 2019; Fenoglio *et al.*, 2021). Moreover, we used two species of the same family (Noctuidae), and negative effects on larval development were found in two other species of this family (van Geffen *et al.*, 2014; Grenis & Murphy, 2019). This means that our results cannot simply be extrapolated to other moth species, but at the

same time they also show that not all species are necessarily negatively affected by ALAN or at least not in the same way.

While the amount of evidence for negative effects of ALAN on larval development in moths is increasing, our study shows that this cannot be generalized across all species. We show evidence for faster larval development and increased body mass under continuous and dynamic ALAN conditions in moths originating from low-medium and high-medium skyglow regions. Further studies are now warranted to explore the mechanisms behind the differences in response between species.

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Data availability

All data and R code used for the analyses are available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.r4xgxd2qm>.

Author contributions

E.V.d.S., M.L., L.L. and H.V.D. contributed to the conceptualisation of this study and the experimental design. E.V.d.S., M.L. and L.L. performed the experimental work and collected the data. E.V.d.S. analysed the data, visualised the results and wrote the original draft. E.V.d.S., R.A.W. and H.V.D. substantially revised the manuscript and all authors approved the final version of the manuscript.

Additional information

The authors declare no conflicts of interest.

Critical note on interpretation of results

In *subsection 7.6.1 of Chapter 7*, we put a critical note on the interpretation of the results as positive for the moths studied.

Appendix C3. Supplementary Information for 3. Experimental study on the impact of continuous and dynamic artificial light at night on moths originating from different skyglow conditions

Authors: Evert Van de Schoot, Marine Lonnoy, Ludovic Laroy, Renate A. Wesselingh and Hans Van Dyck

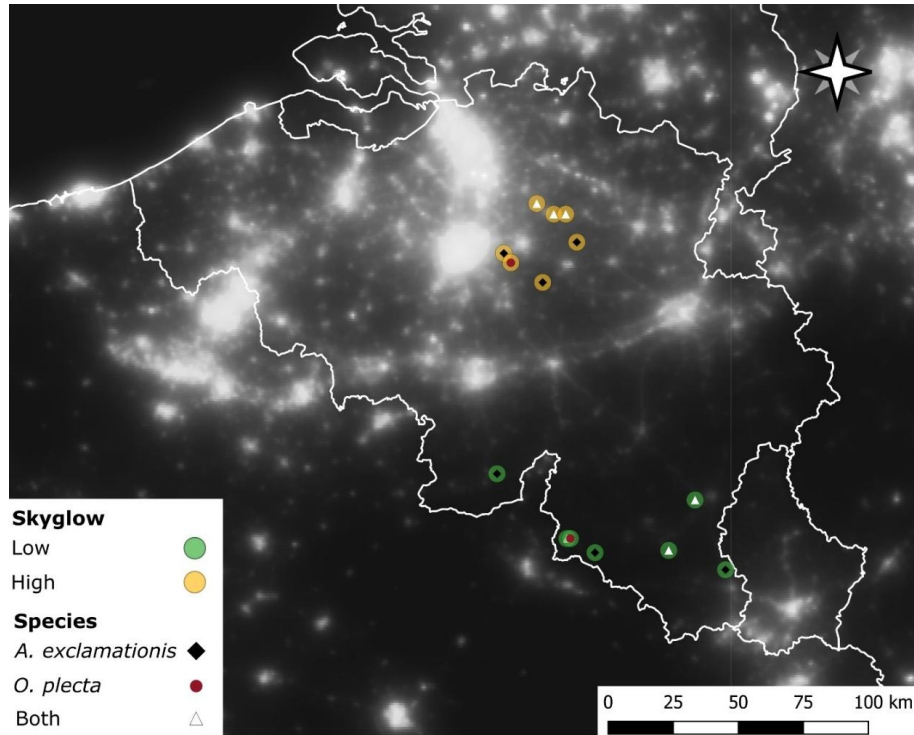


Fig. S3.1. Map of the sampling locations (green and yellow dots) with skyglow data retrieved from Falchi *et al.* (2016). The map was generated in QGIS 3.8.2-Zanzibar (<http://www.qgis.org>).

Table S3.1. Programmed time scheme for the dynamic ALAN treatment, based on traffic data from Belgian cycle highways (retrieved from: <https://fietssnelwegen.be/>).

Timespan (s)	00:00:00	00:31:30	01:00:00	01:43:36	02:00:00	02:42:50	03:00:00
	–	–	–	–	–	–	–
	00:31:30	01:00:00	01:43:36	02:00:00	02:42:50	03:00:00	04:00:00
Cycles	10	9	8	3	5	2	8
Time on (s)	60	60	60	60	60	60	60
Time off (s)	129	130	267	268	454	455	390

Timespan (s)	04:00:00	04:31:24	05:00:00	05:30:00	22:30:00	23:00:00	23:46:00
	–	–	–	–	–	–	–
	04:31:24	05:00:00	05:30:00	22:30:00	23:00:00	23:46:00	00:00:00
Cycles	12	11	12	1	12	40	12
Time on (s)	60	60	60	0	60	60	60
Time off (s)	97	96	90	61200	90	9	10

Table S3.2. Sample sizes for each trait per skyglow level at population of origin, ALAN treatment and sex in *Ochropleura plecta*.

	High-medium skyglow						Low-medium skyglow					
	Control		Continuous		Dynamic		Control		Continuous		Dynamic	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Larval survival	34		34		32		31		32		32	
Duration of larval period	15	10	10	13	13	8	10	11	13	13	14	9
Feeding frequency	15	10	10	13	13	8	10	11	13	13	14	9
Amount eaten	15	10	10	13	13	8	10	11	13	13	14	9
Maximal larval mass	15	10	9	13	13	8	10	11	13	13	14	9
Pupal mass	15	10	10	13	13	8	9	11	10	12	11	8
Adult mass	12	7	8	12	11	8	7	9	13	13	13	8
Mass loss at eclosion	12	7	8	12	11	8	7	9	10	12	10	7

Table S3.3. Sample sizes for each trait per skyglow level at population of origin, ALAN treatment and sex in *Agrotis exclamationis*.

	High-medium skyglow						Low-medium skyglow					
	Control		Continuous ALAN		Dynamic ALAN		Control		Continuous ALAN		Dynamic ALAN	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Larval survival	42		42		42		42		42		42	
Duration of larval period	19	12	17	14	19	12	12	11	13	10	16	12
Feeding frequency	19	12	17	14	19	12	12	11	13	10	16	12
Amount eaten	19	12	17	14	19	12	12	11	13	10	16	12
Maximal larval mass	19	12	17	14	19	12	12	11	13	10	16	12
Pupal mass	19	12	17	14	19	12	12	11	12	10	16	12
Adult mass	18	12	14	13	19	10	11	10	9	10	16	11
Mass loss at eclosion	18	12	14	13	19	10	11	10	8	10	16	11
Growth rate	19	12	17	14	19	12	12	11	13	10	16	12

Table S3.4. Raw mean values $\pm$ SE and statistical output for differences in larval survival and development between *Ochropleura plecta* and *Agrotis exclamationis*. 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.

	<i>O. plecta</i>	<i>A. exclamationis</i>	χ^2	P
Larval survival (%)	74.87 $\pm$ 3.11	67.46 $\pm$ 2.96	2.23	0.136
Duration of larval period (days)	15 $\pm$ 0	47 $\pm$ 1	284.59	< 0.001
Feeding frequency (%)	83.54 $\pm$ 0.58	80.79 $\pm$ 0.44	15.97	< 0.001
Amount eaten (food units)	15.1 $\pm$ 0.3	62.0 $\pm$ 1.7	446.18	< 0.001
Maximal larval mass (mg)	265.33 $\pm$ 6.95	741.73 $\pm$ 11.48	294.42	< 0.001
Pupal mass (mg)	149.86 $\pm$ 1.97	351.46 $\pm$ 5.94	138.88	< 0.001
Adult mass (mg)	84.31 $\pm$ 1.39	206.62 $\pm$ 4.05	234.46	< 0.001
Mass loss at eclosion (%)	45.11 $\pm$ 0.70	42.15 $\pm$ 0.69	6.22	0.013

CHAPTER 4

Evolutionary change in flight-to-light response in urban moths comes with changes in wing morphology

Authors: Evert Van de Schoot, Thomas Merckx, Dieter Ebert, Renate A. Wesselingh, Florian Altermatt and Hans Van Dyck

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In this chapter, we address the hypothesis that reduction in flight-to-light behaviour is related to lower mobility. We investigate whether flight-related morphology differs between urban light-polluted populations and rural dark populations, and whether potential changes relate to the flight-to-light response observed by Altermatt and Ebert (2016).

Abstract

Moths and other insects are attracted by artificial light sources. This flight-to-light behaviour disrupts their general activity focused on finding resources, such as mating partners, and increases predation risk. It thus has substantial fitness costs. In illuminated urban areas, spindle ermine moths *Yponomeuta cagnagella* were reported to have evolved a reduced flight-to-light response. Yet, the specific mechanism remained unknown, and was hypothesized to involve either changes in visual perception or general flight ability or overall mobility traits. Here, we test whether spindle ermine moths from urban and rural populations—with known differences in flight-to-light responses—differ in flight-related morphological traits. Urban individuals were found to have on average smaller wings than rural moths, which in turn correlated with a lower probability of being attracted to an artificial light source. Our finding supports the reduced mobility hypothesis, which states that reduced mobility in urban areas is associated with specific morphological changes in the flight apparatus.

Introduction

Ongoing urbanization is a textbook example of the ever-increasing human impact on the environment. The United Nations (2019) predicts that more than two-thirds of the world's population will live in urban areas by 2050, driving strong expansion of the urban land area (UN-Habitat, 2022). For many species, urbanization goes hand in hand with a deterioration of environmental quality caused by diverse processes, one of them being light pollution. Since the review by Longcore and Rich in 2004, the interest for the consequences of light pollution caused by artificial light at night (ALAN)—has strongly increased, particularly for its effects on nocturnal insects (Owens & Lewis, 2018; Owens *et al.*, 2020; Boyes *et al.*, 2021b; Grubisic & van Grunsven, 2021; Kühne *et al.*, 2021; Kehoe *et al.*, 2022). ALAN mainly affects insects in two ways. Firstly, it alters day–night cycles, disrupting life cycle regulation (e.g., disrupted diapause induction: van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Merckx *et al.*, 2023) and changing plant–pollinator interactions (Knop *et al.*, 2017; Macgregor *et al.*, 2019; Wilson *et al.*, 2021). Secondly, many insects experience negative consequences from their innate positive or negative phototaxis, causing them to be attracted (Fabian *et al.*, 2024) or repelled (Farnworth *et al.*, 2018) by ALAN. This, in turn, leads insects away from their favourable habitats (Frank, 2006) and can result in higher predation risk. Nocturnal insects are also distracted or restrained from essential behaviours like foraging (van Langevelde *et al.*, 2017) and

reproduction (van Geffen *et al.*, 2015b). These changes do not only result in ecological alteration, but may also operate as selective agents potentially driving rapid evolution, which may lead to phenotypic divergence between urban and rural populations (Swaddle *et al.*, 2015; Hopkins *et al.*, 2018). In insects, and especially Lepidoptera, selection on flight performance is usually associated with changes in morphology, including body mass, thorax mass (containing the flight muscles), wing size, wing shape and wing loading (Berwaerts *et al.*, 2002; Frazier *et al.*, 2008; Flockhart *et al.*, 2017). Merckx *et al.* (2018) showed intraspecific shifts towards larger and thus more mobile individuals in urban macro-moth populations. However, their study did not specifically test for the effect of ALAN. Furthermore, selection on flight behaviour stemming from changes in light environments might differ across species (Cribellier *et al.*, 2022).

Altermatt and Ebert (2016) showed experimentally that spindle ermine moths (*Yponomeuta cagnagella*) from urban populations showed a reduced attraction to light compared to individuals from rural populations. Moths originating from light-polluted urban areas, although reared under common-garden settings, had a 30 % weaker flight-to-light response than conspecifics from pristine dark areas. These results suggest evolution of this trait in urban environments, reducing an ALAN-mediated ecological trap effect. Altermatt and Ebert (2016) discussed two mutually non-exclusive mechanisms explaining the observed patterns: first, a decreased perception of light (see also Fabian *et al.*, 2024); and second, a reduced overall mobility in urban moths, which could also result from a (non-adaptive) by-product of selection on other traits. Here, we used the specimens from this previous study to investigate changes in flight-related morphology of ermine moths in urban areas and test for their propensity to flight to the light.

Material and methods

Study species and sampling sites

We used adults of the spindle ermine moth *Yponomeuta cagnagella* (Hübner) (Lepidoptera: Yponomeutidae) to study differences in flight-related morphological traits between individuals from rural *versus* urban populations, reared under common-garden settings. This small moth species is common in Europe and West Asia. Adults fly from the end of June to October. Caterpillars of *Y. cagnagella* are the only species in the *Yponomeuta* species complex to feed monophagously on spindle trees (*Euonymus* spp.) and especially *Euonymus europaeus* L. is frequently used as a host plant. We

analysed specimens used in the experiment of Altermatt and Ebert (2016), which were stored at -20°C after the flight-to-light experiment.

In the original experiment, second-instar larvae were collected on *Euonymus europaeus* in 11 populations in Switzerland and France. Five populations were located in urbanized areas with high levels of ALAN (radiance (L) $> 40 \times 10^{-9} \text{ W m}^{-2} \text{ sr}^{-1}$) while six populations were located in dark, rural areas (L $< 3 \times 10^{-9} \text{ W m}^{-2} \text{ sr}^{-1}$) (Fig. S4.1, Appendix C4). For each population, larvae from one to six full-sib families were reared under common-garden conditions in the lab. Two to 3 days after eclosion, adult moths were individually colour-marked on the wings and their flight-to-light response was tested. Moths were released at one side of a walk-in cage (bottom: $5.7 \times 2.5 \text{ m}$, top: $5.7 \times 1.8 \text{ m}$, height: 3 m) with a Heath actinic (6 W) light trap at the opposite end. Eight hours after release, the light trap was checked for captured moths. Both captured and non-captured moths were counted, collected and stored in a freezer (-20°C) (see Altermatt and Ebert (2016) for more details). Morphological analyses were done at UCLouvain (N = 680, a few individuals could no longer be identified due to loss of colour marking).

Flight-related morphology

Thorax and abdomen mass

The moths were placed in an incubator at 60°C for 4 h. Preliminary tests had shown that dry body mass reached stable values after this period. Because (parts of) antennae and legs were often lacking from dried specimens, antennae and legs were systematically removed from all individuals before measuring total dry body mass (m_{tot}) with a microbalance (Mettler MT5; precision $\pm 0.001 \text{ mg}$). We separated head, thorax, abdomen and wings with needle and tweezers and determined the thorax (m_{th}) and abdomen mass (m_{ab}). Relative thorax ($m_{\text{th,rel}}$) and abdomen mass ($m_{\text{ab,rel}}$) were calculated by dividing by total dry body mass.

Wing morphology

We took standardized pictures (Olympus TG-6 camera) of the ventral side (where a clear difference between wing surface and fringe is visible) of the right forewing (Fig. 4.1). In the case of significant wing damage, the left forewing was used instead. Forewing length (FWL) (from the far left to right point of the dark grey zone), forewing width (FWW) (from the outermost (highest) point of the costa in a line perpendicular to the dorsal edge) and forewing area (A) were measured using ImageJ software (<https://imagej.net/ij/index.html>) on size-calibrated pictures. Length and width were measured twice and the mean value was used in the analyses.

From these wing measures, we calculated aspect ratio (AR) as $4 \cdot \text{FWL}^2 / \text{FWW}$ and wing loading (WL) as m_{tot} / A (Berwaerts *et al.*, 2002; Van Dyck & Wiklund, 2002). The measurements were made without knowing the origin of the animals.

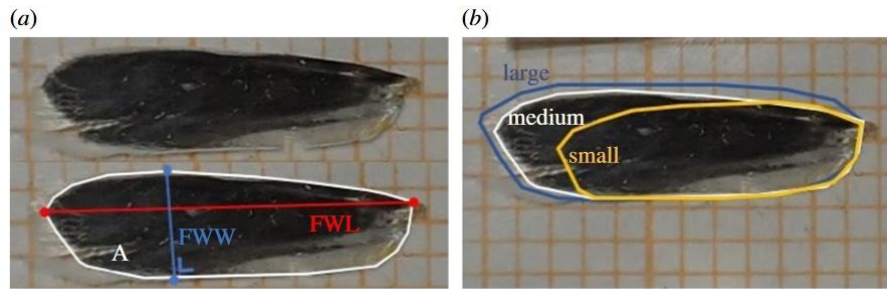


Fig 4.1. (a) *Yponomeuta cagnagella* forewing indicating the three morphological measurements taken: area (A), forewing length (FWL) and forewing width (FWW). (b) Contours of medium-sized forewing (white) with contours of relatively large (blue) and small (yellow) wings, respectively. Orange grid lines in the background indicate a millimetre scale.

Statistical analysis

We tested for differences in morphological traits between samples from light polluted (urban) and dark (rural) population origin, using linear mixed effect regression models. Analyses were done separately for both sexes, since there was strong collinearity between the factors ‘sex’ and ‘body mass’ (females are heavier than males), body mass being also allometrically correlated with several of the morphological traits. For the analysis of the relationship between flight-to-light response and morphology, generalized linear mixed models with a binomial error distribution were used. Total body mass (m_{tot}) was included as a covariate, except in models with $m_{\text{th,rel}}$, $m_{\text{ab,rel}}$ and WL. Family identity nested within population identity was used as a random factor in all models. All analyses were performed in R 4.2.2 (R Development Core Team, 2022). We adopted the language of evidence in the results section (Muff *et al.*, 2022). Raw means and SE’s are reported in the electronic supplementary material (Table S4.1 and Fig. S4.2, Appendix C4).

Results

We have strong evidence that female moths from light-polluted, urban origins had narrower wings (on average by 2 %) and higher aspect ratio (by

1.5 %) than rural-origin females from dark night conditions (Table 4.1, Fig. 4.2a,b). Urban females also had smaller wing areas compared to rural females, but with weaker evidence (Table 4.1, Fig. 4.2c). Relative abdomen mass was on average 2.5 % lower in urban females, again with weaker evidence, while total body mass, relative thorax mass and wing loading showed no significant differences (Table 4.1).

We tested whether the morphological traits are related to the flight-to-light response. Females with shorter, narrower and smaller wings and higher wing loading showed a weaker flight-to-light response (strong evidence) (Table 4.2, Fig. 4.2d–f), especially when they originated from urban populations (Wald $\chi^2 = 6.17$, $p = 0.013$); in rural-origin females the same relationship was found, but weaker (Wald $\chi^2 = 2.90$, $p = 0.088$). Mass-related traits and aspect ratio did not show a correlation with the flight-to-light response (Table 4.2).

Male moths showed qualitatively similar morphological differences: urban males had shorter (by 1.4 %), narrower (by 2.5 %) and smaller wings (by 3.9 %) than rural males (strong evidence) (Table 4.1, Fig. 4.2a–c). The smaller wing area and the slightly higher body mass in urban males led to higher wing loadings, with strong evidence (Table 4.1). No significant differences were found for relative thorax and abdomen mass and forewing aspect ratio in males either (Table 4.1). Smaller-winged males tended to show a weaker flight-to-light response (Table 4.2, Fig. 4.2f). This tendency is mainly driven by the difference in wing length between rural and urban moths (Tables 4.1 and 2, Fig. 4.2d,e). Other morphological traits did not show significant relations with flight-to-light response (Table 4.2).

Table 4.1. Differences in flight-related morphology between rural and urban spindle ermine moths. For each morphological trait the estimated mean $\pm$ SE (n) is given. All tests are based in 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.

	Female				Male			
	Rural	Urban	Wald X ²	P	Rural	Urban	Wald X ²	P
Total body mass (mg)	12.871 $\pm$ 0.445 (182)	13.362 $\pm$ 0.473 (159)	0.57	0.450	7.674 $\pm$ 0.251 (147)	8.329 $\pm$ 0.258 (192)	3.31	0.069°
Relative thorax mass	0.214 $\pm$ 0.005 (182)	0.222 $\pm$ 0.005 (159)	1.23	0.267	0.269 $\pm$ 0.006 (147)	0.262 $\pm$ 0.006 (190)	0.87	0.350
Relative abdomen mass	0.697 $\pm$ 0.007 (182)	0.680 $\pm$ 0.007 (159)	3.16	0.076°	0.605 $\pm$ 0.007 (147)	0.614 $\pm$ 0.007 (192)	0.74	0.390
Wing length (mm)	10.702 $\pm$ 0.045 (176)	10.641 $\pm$ 0.048 (143)	0.86	0.354	10.516 $\pm$ 0.052 (138)	10.369 $\pm$ 0.050 (180)	4.11	0.043
Wing width (mm)	3.089 $\pm$ 0.014 (181)	3.027 $\pm$ 0.015 (157)	8.88	0.003	2.979 $\pm$ 0.014 (147)	2.904 $\pm$ 0.014 (191)	13.80	< 0.001
Wing area (mm²)	29.047 $\pm$ 0.225 (179)	28.422 $\pm$ 0.236 (146)	3.66	0.056°	27.269 $\pm$ 0.199 (140)	26.220 $\pm$ 0.192 (182)	14.19	< 0.001
Aspect ratio	15.764 $\pm$ 0.072 (176)	15.998 $\pm$ 0.077 (141)	4.93	0.026	16.243 $\pm$ 0.092 (138)	16.422 $\pm$ 0.089 (179)	1.91	0.167
Wing loading (mg mm⁻²)	0.446 $\pm$ 0.011 (179)	0.466 $\pm$ 0.011 (146)	1.69	0.194	0.285 $\pm$ 0.007 (140)	0.315 $\pm$ 0.007 (182)	10.00	0.002

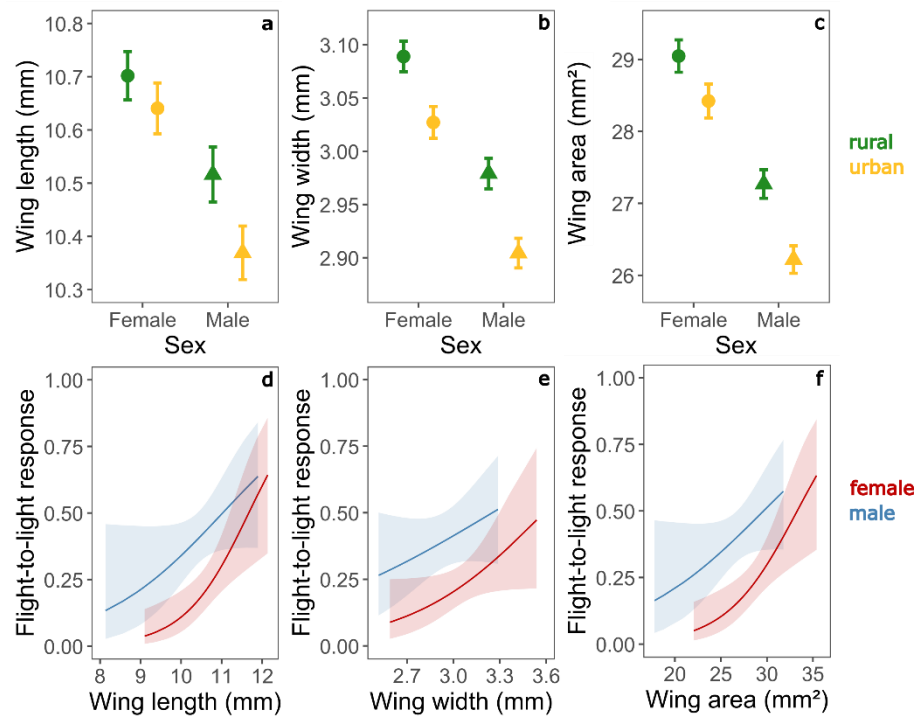


Fig. 4.2. (a–c) Predicted values $\pm$ SE of wing length, wing width and wing area in female and male spindle ermine moths (*Yponomeuta cagnagella*) from rural and urban populations. (d–f) Predicted effects and 95 % confidence intervals (shaded area) of wing length, wing width and wing area on flight-to-light response for females and males.

Table 4.2. Statistical test results for correlations with flight-to-light response for each morphological trait in *Yponomeuta cagnagella*. Significant *p*-values (< 0.05) are given in bold and statistical trend values (< 0.1) are indicated with a ° symbol. All tests are based on d.f. = 1.

	Female		Male	
	Wald X ²	P	Wald X ²	P
Total body mass	0.69	0.271	0.69	0.451
Relative thorax mass	0.00	0.988	0.00	0.974
Relative abdomen mass	1.11	0.293	0.22	0.635
Wing length	9.92	0.002	3.36	0.067°
Wing width	3.63	0.057°	1.62	0.219
Wing area	9.27	0.002	3.04	0.081°
Aspect ratio	2.19	0.139	0.28	0.599
Wing loading	8.61	0.003	2.23	0.135

Discussion

Urban spindle ermine moths have reduced flight-to-light response compared to rural moths, and it has been hypothesized that such an evolutionary response may be driven by reduced mobility associated with morphological changes (Altermatt & Ebert, 2016). Here, we provide evidence for this reduced mobility hypothesis by contrasting flight-related morphology of urban moth populations that evolved under ALAN conditions and rural, dark-night populations. Urban moths had on average smaller wings, which in turn correlated with a lower probability of being attracted to an artificial light source.

Mobility and dispersal, and associated behaviours, are known to be under strong selection (e.g., Fronhofer & Altermatt, 2015; Fronhofer *et al.*, 2015), because they are associated with foraging, mating and dispersal. Effects of urbanization on mobility-related morphology have been found for some organisms, such as *Anolis* lizards (Winchell *et al.*, 2016, 2018). In insects, wing size and aspect ratio are generally considered to play a key role in flight performance and are positively related to acceleration (Berwaerts *et al.*, 2002) and dispersal capacity (Jyothi *et al.*, 2021; Cribellier *et al.*, 2022). High wing loading leads to increased flight and dispersal capacity, but also to decreased manoeuvrability (Le Roy *et al.*, 2019). Therefore, flight-related morphological traits are expected to be under selection. Our findings suggest that urban moths might have reduced acceleration and dispersal capacity compared to rural moths and that urban males may have reduced manoeuvrability due to increased wing loading.

A confounding factor of flight-related traits can be body and thorax size, which often covary positively with wing traits. However, we did not find changes in body size in urban populations. Independence of wing morphology and body size is also supported by a study on the noctuid moth *Agrotis exclamationis*, where body size, but not wing length, increased over 137 years of urbanization (Keinath *et al.*, 2021), possibly leading to higher mobility (Merckx *et al.*, 2018). However, this study was based on museum voucher specimens, and differences could thus be due to plasticity effects or non-random sampling. Furthermore, selection regimes on flight behaviour may act differently on this generalist species with high mobility.

We acknowledge that other traits may also have been under selection during adaptation to urban environments, for example compound eye morphology and physiology (Altermatt & Ebert, 2016; Keinath *et al.*, 2021). We could not measure eye morphology, yet follow-up studies may address these and other traits in *Y. cagnagella* as well. The moths used in the experiments were collected as larvae in their respective environments. If the traits measured were influenced by maternal effects or very early juvenile experience, the argument for genetic adaptation would need to be re-considered. Two-generation common-garden experiments would allow the effects of maternal phenotype, phenotypic plasticity and genetics to be disentangled.

Habitat fragmentation is an important aspect of current global change and a typical consequence of urbanization. It can trigger both adaptive and non-adaptive evolutionary change (Johnson & Munshi-South, 2017). Food specialists, such as *Y. cagnagella*, can adapt to habitat fragmentation by changing their mobility (Hahs *et al.*, 2023). When the distribution of suitable habitat is highly fragmented, reduced inter-patch dispersal capacity can be associated with higher fitness (Cheptou *et al.*, 2008). This, combined with the negative effects of light pollution, may have promoted the evolution of reduced mobility (Hahs *et al.*, 2023). Modified mobility patterns in urbanized, light-polluted populations may also emerge as by-products of selection on other life-history traits. Although there is evidence that dispersal behaviour can evolve independently of other life-history traits (Bonte & Doherty, 2017), the movement patterns we observed may relate to daily or routine movements rather than dispersal per se. Further study is now warranted on the behavioural nature of the flights in both males and females. Reduced mobility would in turn reduce gene flow between populations, making them more vulnerable to the consequences of genetic drift. Besides such effects on (meta-)population viability, monitoring schemes using light traps are affected too (Altermatt & Ebert, 2016): in addition to reduced contrast and hence reduced flight-to-light response in light-polluted areas, moths have species-specific attraction radii (Merckx & Slade, 2014) that may become

smaller following ALAN-driven reduced mobility, further reducing flight-to-light response. This implies that negative population trends obtained from light-trap based monitoring schemes in light-polluted regions could partly be due to physical and evolved trapping bias, yet the extent of this is not known.

As the negative effects of light pollution on the ecology of many species become apparent, it becomes important to understand to what extent organisms may evolve in response to these new conditions. Altermatt and Ebert (2016) provided evidence for this by demonstrating a reduced flight-to-light response in urban moths, and we have shown that this is related to changes in wing morphology. The negative effects of light pollution highlight that in urban landscapes we need to strive for green and dark corridors that can functionally connect populations of less mobile species.

Data accessibility

All data and R code used for the analyses are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qz612jmp5>. Electronic supplementary material is available online (Van de Schoot *et al.*, 2024: Chapter 4).

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Author contributions

E.V.d.S.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft, writing—review and editing; T.M.: conceptualization, formal analysis, supervision, writing—original draft, writing—review and editing; D.E.: conceptualization, resources, writing—original draft, writing—review and

editing; R.A.W.: conceptualization, formal analysis, supervision, writing—review and editing; F.A.: conceptualization, data curation, formal analysis, funding acquisition, resources, supervision, writing—original draft, writing—review and editing; H.V.D.: conceptualization, formal analysis, funding acquisition, project administration, resources, supervision, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration

We declare we have no competing interests.

Critical note on cause morphological changes

In *subsection 7.6.2 of Chapter 7*, we discuss other potential causes for the observed differences in flight-related morphology.

Appendix C4. Supplementary Information for 4. Evolutionary change in flight-to-light response in urban moths comes with changes in wing morphology

Authors: Evert Van de Schoot, Thomas Merckx, Dieter Ebert, Renate A. Wesselingh, Florian Altermatt and Hans Van Dyck

Table S4.1. Statistical output showing differences in flight-related morphology between rural and urban individuals for both sexes. For each morphological trait the raw mean $\pm$ SE is given, as well as the number of measured individuals between brackets. All tests are based on $df = 1$. Significant P-values (<0.05) are given in bold, whereas statistical trend values (<0.1) are highlighted with a ° symbol.

	Female				Male			
	Rural	Urban	Wald χ^2	P	Rural	Urban	Wald χ^2	P
Total body mass (mg)	12.755 $\pm$ 0.149 (182)	13.517 $\pm$ 0.158 (159)	0.57	0.450	7.732 $\pm$ 0.106 (147)	8.473 $\pm$ 0.097 (192)	3.31	0.069°
Relative thorax mass	0.214 $\pm$ 0.003 (182)	0.220 $\pm$ 0.003 (159)	1.23	0.267	0.268 $\pm$ 0.004 (147)	0.261 $\pm$ 0.003 (190)	0.872	0.350
Relative abdomen mass	0.696 $\pm$ 0.003 (182)	0.681 $\pm$ 0.005 (159)	3.16	0.076°	0.606 $\pm$ 0.004 (147)	0.616 $\pm$ 0.005 (192)	0.74	0.390
Wing length (mm)	10.669 $\pm$ 0.032 (176)	10.664 $\pm$ 0.038 (143)	0.86	0.354	10.433 $\pm$ 0.042 (138)	10.440 $\pm$ 0.034 (180)	4.11	0.043
Wing width (mm)	3.080 $\pm$ 0.010 (181)	3.040 $\pm$ 0.011 (157)	8.88	0.003	2.958 $\pm$ 0.011 (147)	2.922 $\pm$ 0.010 (191)	13.80	<0.001
Wing area (mm²)	28.919 $\pm$ 0.163 (179)	28.607 $\pm$ 0.172 (146)	3.66	0.056°	26.830 $\pm$ 0.177 (140)	26.559 $\pm$ 0.154 (182)	14.19	<0.001
Aspect ratio	15.745 $\pm$ 0.045 (176)	15.964 $\pm$ 0.061 (141)	4.93	0.026	16.246 $\pm$ 0.056 (138)	16.444 $\pm$ 0.052 (179)	1.91	0.167
Wing loading (mg/mm²)	0.441 $\pm$ 0.004 (179)	0.470 $\pm$ 0.005 (146)	1.69	0.194	0.285 $\pm$ 0.003 (140)	0.319 $\pm$ 0.003 (182)	10.00	0.002

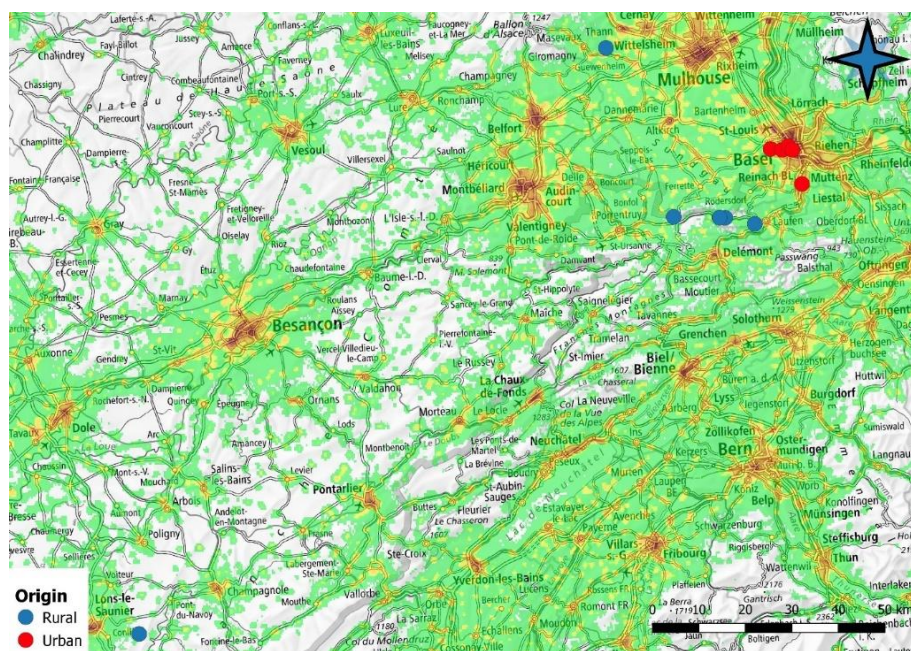


Fig. S4.1. Map of the sampling locations (blue and red dots) with radiance data retrieved from www.lightpollutionmap.info. Transparent and green regions have very low levels of light pollution. Red and yellow regions have high levels of light pollution.

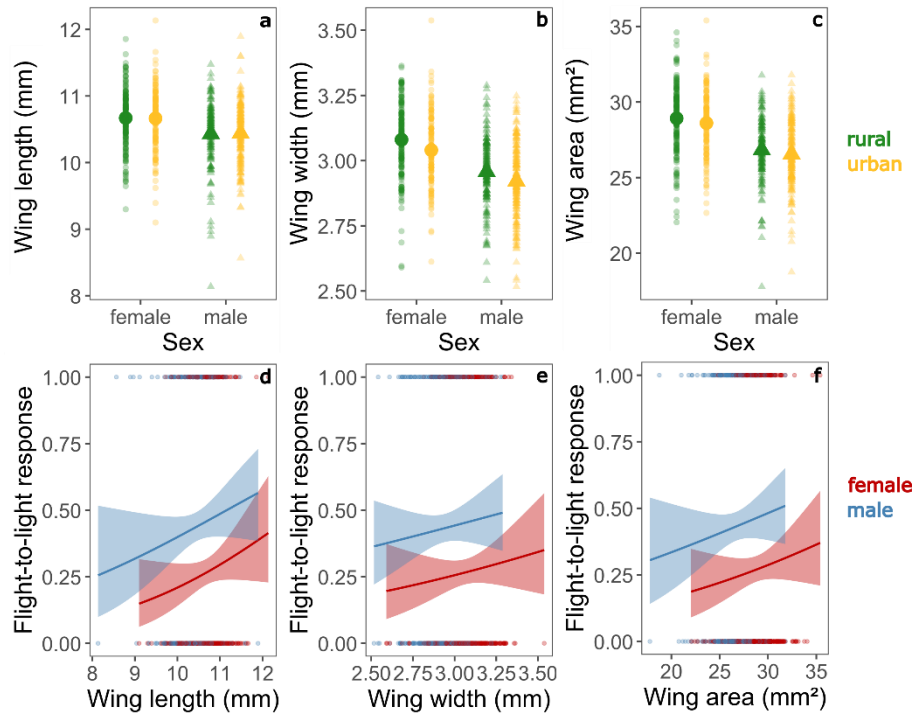


Fig. S4.2. **A-C** Raw values of wing length, wing width and wing area in females and males originating from rural and urban populations. Large dots and triangles show the mean value. **D-F** Raw values and smoothed binomial regression lines (*geom_smooth(method = "glm", method.args = list(family = "binomial"))*) (and 95 % confidence intervals: shaded area) of wing length, wing width and wing area on flight-to-light response in females and males.

CHAPTER 5

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

Authors: Evert Van de Schoot, Christophe Pels, Renate A. Wesselingh and
Hans Van Dyck

This chapter has been submitted.

In this chapter, we build on the results of *Chapter 3 and 4* by studying the impact of larval development under dynamic and continuous ALAN on flight and fecundity-related morphology as well as wing melanisation. We also address whether responses are sex-specific and explore potential adaptive responses in populations originating from higher skyglow conditions.

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 changed 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. Our results suggest consequences for adult flight behaviour and fitness in this moth species.

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; Warrant *et al.*, 2024), 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 (Warrant *et al.*, 2024). 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: Chapter 3) and therefore also body mass (van Geffen *et al.*, 2014; Durrant *et al.*, 2018; Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025c: Chapter 2, 2025a: Chapter 3).

Sexual dimorphism is a widespread phenomenon in animals, including insects (Shine, 1989). 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: Rohner *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; Söber *et al.*, 2019). More subtle differences may stem from differences in weight loss during adult eclosion (Molleman *et al.*, 2011; Van de Schoot *et al.*, 2025a: Chapter 3). 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.*, 2025c: Chapter 2, 2025a: Chapter 3). 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: Chapter 4) 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.*, 2015b; 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).

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. exclamatoris* showed that larval development under ALAN resulted in increased body mass (Van de Schoot *et al.*, 2025a: Chapter 3). 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: Chapter 4). 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. exclamatoris* 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.*, 2025c: Chapter 2). Previous work by Van de Schoot *et al.* (2025a: Chapter 3) on *A. exclamatoris* 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: Chapter 4), 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.

Material and methods

Study species and female sampling

The heart and dart *Agrotis exclamatoris* 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: Chapter 3). 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>; Fig. S5.1, Appendix C5). 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 rearing experiment

Six to twelve larvae per family were transferred to a single plastic box per individual with aeration holes and a piece of paper towel. 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 S5.1, Appendix C5); (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

Thorax and abdomen mass

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 $\pm 10^{-2}$ 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 Fig. S5.2 (Appendix C5). Aspect ratio was calculated as $4 \cdot \text{FWL}^2/\text{FWW}$ and wing loading as $m_{\text{tot}}/\text{FWA}$ (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) (Fig. S5.2, Appendix C5).

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 (Muff *et al.*, 2022).

Results

Table 5.1 summarizes the statistical output. Females were heavier 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 increased significantly under continuous ALAN, as it did in females, it did not increase under dynamic ALAN (continuous ALAN–dynamic ALAN: $t_{128} = 3.47$, $p = 0.001$; continuous ALAN–control: $t_{127} = 4.00$, $p < 0.001$; Fig. 5.1a). 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 (Fig. 5.1b-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: $t_{128} = 3.99$, $p < 0.001$; Fig. 5.1b-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 (Fig. 5.2a). 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 (Fig. 5.2b,d), and there was some evidence for longer forewings in moths originating from low-medium skyglow compared to high-medium skyglow populations (Fig. 5.2c). 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 (Fig. 5.2e). Females clearly had higher wing loadings than males (Fig. 5.2f).

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 (Fig. 5.3).

Table 5.1. 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°
Forewing width	Total body mass	96.54	< 0.001
	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°

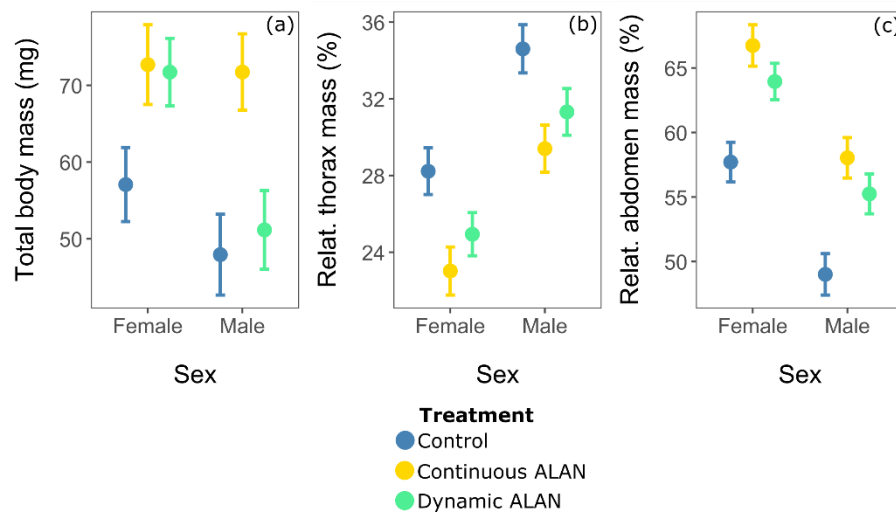


Fig. 5.1. Model parameter estimates $\pm$ SE of total body mass and relative thorax and abdomen mass in female and male *Agrotis exclamator* under the three ALAN treatments.

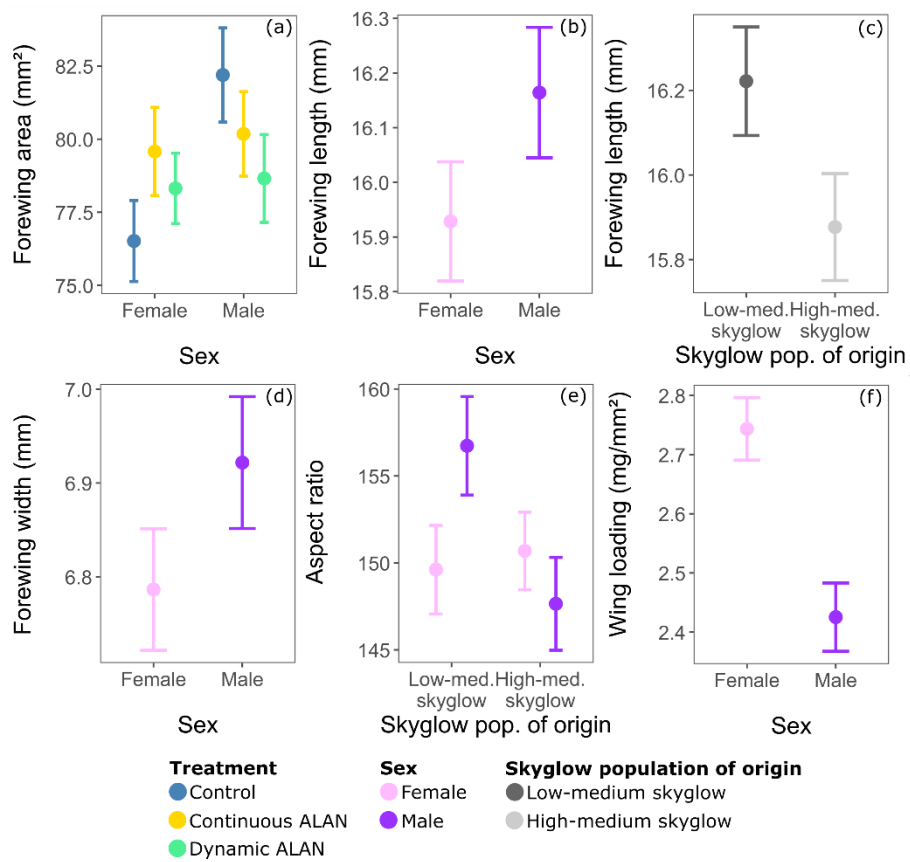


Fig. 5.2. Model parameter estimates $\pm$ SE of wing morphology in female and male *Agrotis exclamationis* originating from low-medium and high-medium skyglow populations under the three ALAN treatments.

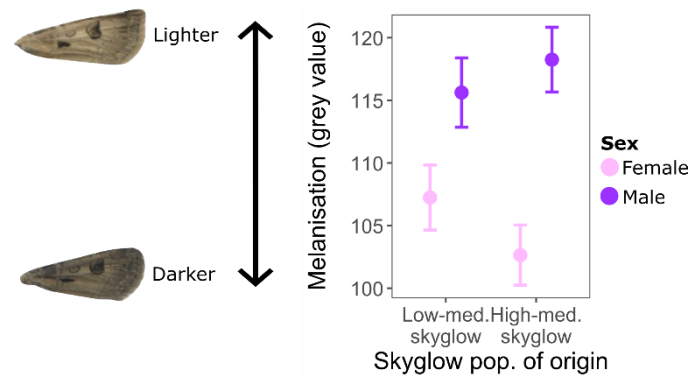


Fig. 5.3. Model parameter estimates $\pm$ SE of dorsal forewing melanisation in female and male *Agrotis exclamationis* originating from low-medium and high-medium skyglow populations. Lower grey values signify darker colour (i.e., higher melanisation).

Discussion

Two previous studies have investigated the impact of light pollution in *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: Chapter 3) 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: *Chapter 3*). 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: *Chapter 3*). 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: *Chapter 4*). 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: *Chapter 4*), 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; Garriss & 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. exclamatoris* 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.*, 2025c: Chapter 2).

As expected, we found the known sexual colour dimorphism in *A. exclamatoris* 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 (Van de Schoot *et al.*, 2025b: Chapter 6), 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: Chapter 4). 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. exclamatoris*. 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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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.

Conflict of interest declaration

The authors declare no conflicts of interest.

Appendix C5. Supplementary Information for 5. Larval development under continuous and dynamic light pollution alters sexual dimorphism in a moth

Authors: Evert Van de Schoot, Christophe Pels, Renate A. Wesselingh and Hans Van Dyck

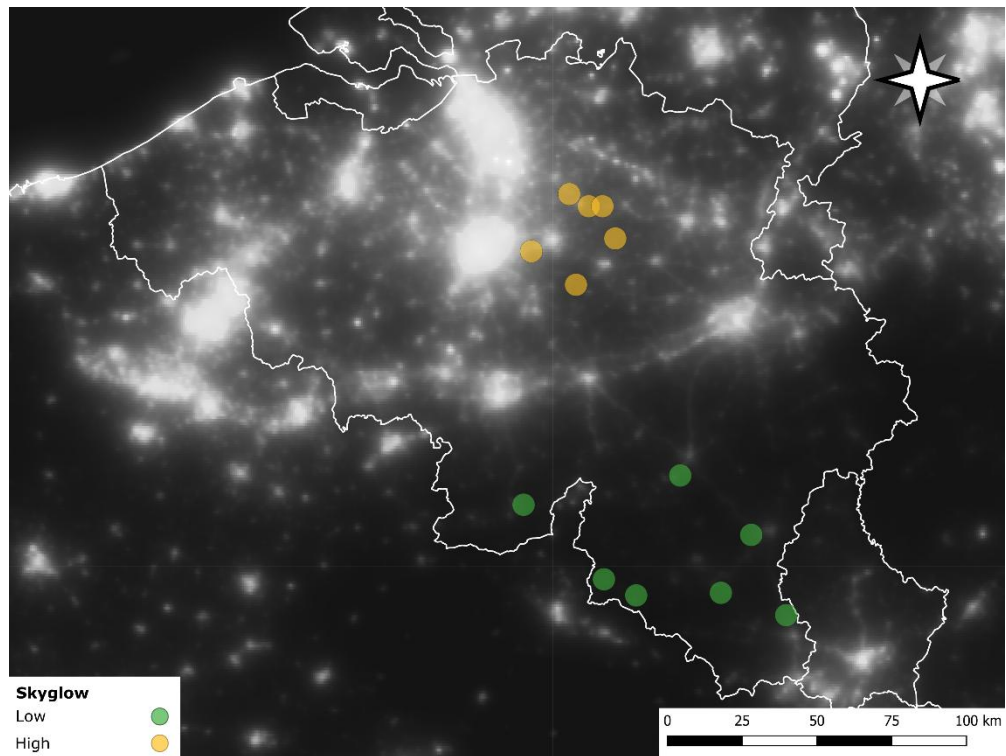


Fig. S5.1. Map of the sampling locations (green and yellow dots) with skyglow data retrieved from Falchi *et al.* (2016).

Table S5.1. Programmed time scheme for the dynamic ALAN treatment, based on traffic data from Belgian cycle highways (retrieved from: <https://fietssnelwegen.be/>).

Timespan (s)	00:00:00	00:31:30	01:00:00	01:43:36	02:00:00	02:42:50	03:00:00
	–	–	–	–	–	–	–
	00:31:30	01:00:00	01:43:36	02:00:00	02:42:50	03:00:00	04:00:00
Cycles	10	9	8	3	5	2	8
Time on (s)	60	60	60	60	60	60	60
Time off (s)	129	130	267	268	454	455	390

Timespan (s)	04:00:00	04:31:24	05:00:00	05:30:00	22:30:00	23:00:00	23:46:00
	–	–	–	–	–	–	–
	04:31:24	05:00:00	05:30:00	22:30:00	23:00:00	23:46:00	00:00:00
Cycles	12	11	12	1	12	40	12
Time on (s)	60	60	60	0	60	60	60
Time off (s)	97	96	90	61200	90	9	10

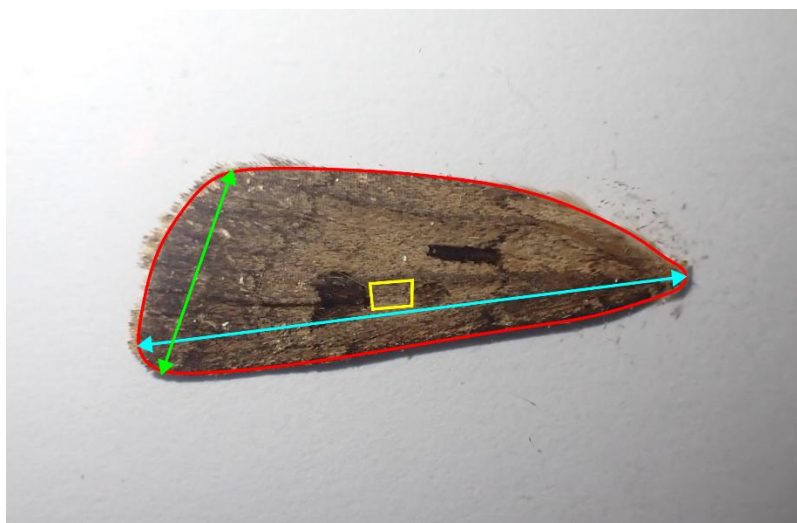


Fig. S5.2. Example forewing of *A. exclamationis* showing the delineations of the morphological measurements. Red: wing area, blue: wing length, green: wing width, yellow: zone for measuring melanisation.

CHAPTER 6

Skyglow and especially direct streetlight pollution alter moth communities

Authors: Evert Van de Schoot, Renate A. Wesselingh and Hans Van Dyck

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In this chapter, we use a full-factorial study design to simultaneously investigate the impact of skyglow and direct light pollution by streetlights on moth communities. We address the impact on moth abundance, species richness, diversity and community composition. Further, we explore general patterns independent from species identity with a trait-based analysis.

Abstract

Light pollution caused by artificial light at night (ALAN) affects biodiversity worldwide and is still increasing. Species vary in their response to ALAN, but the impact on communities remains poorly understood. Effects of indirect light pollution by skyglow and direct streetlight pollution on communities have usually been addressed separately, and in most studies so far, urbanisation levels are a confounding factor for ALAN effects *per se*. Here, we sampled garden moth communities according to a study design that integrated two levels of direct streetlight pollution and two regional skyglow levels to test for additive effects of both types of ALAN. We also tested whether ALAN conditions related to community changes in species' morphological, behavioural and life-history traits.

Both skyglow and streetlights negatively affected moth abundance. Species richness and diversity decreased under direct streetlight, independent of skyglow levels. Both types of ALAN affected moth community composition and we identified several relationships with species traits in the local moth communities. Skyglow filtered for hibernating stage and larval habitation, while streetlight pollution filtered for voltinism, larval food specificity, habitat openness and hibernating stage.

Our study provides evidence that both skyglow and, more strongly, streetlight pollution affect moth communities. A significant decline in moth abundance will have consequences for ecosystem functioning through reduced food availability for predators and diminished pollinator services. At the community level, ALAN operates as a filter for species and species traits, and based on our results, we argue that future studies should consider both skyglow and direct light pollution.

Introduction

Artificial light at night (ALAN) illuminates significant parts of the natural and anthropogenic environment worldwide (Falchi *et al.*, 2016). ALAN continues to reach new areas and increase in intensity (Kyba *et al.*, 2017, 2023; Guetté *et al.*, 2018). The potential of light pollution as a biodiversity threat has long been underestimated, but in the last decades, particularly since the seminal review by Longcore and Rich (2004), ALAN has received growing attention as a global biological issue in the field of sensory ecology and evolution (Dominoni *et al.*, 2020a). Light pollution is generally divided into direct influence from light sources such as streetlights, and skyglow, which is the reflection of artificial light due to aerosols present in the atmosphere in an indirect and diffuse way (Jechow *et al.*, 2017). Direct light pollution brightens

an area at the local scale and can cause a high level of heterogeneity in an environment, whereas skyglow can spread hundreds of kilometres from its source (Falchi *et al.*, 2016).

Light pollution affects animals at different levels of biological organisation, from the disturbance of physiological cycles (e.g., melatonin suppression: Grubisic *et al.*, 2019), impact on growth (e.g., Luarte *et al.*, 2016b; Dananay & Benard, 2018; Owens *et al.*, 2020), to the alteration of circadian activity patterns of organisms (e.g., Dominoni *et al.*, 2020b; Hermans *et al.*, 2024). Furthermore, ALAN can change behaviour in different animal groups (O'Connor *et al.*, 2019; Elgert *et al.*, 2020; Grunst *et al.*, 2023; Fabian *et al.*, 2024). Finally, light pollution has been shown to modify predator-prey interactions, usually in favour of predators, for example through locally increased prey abundance (Willmott *et al.*, 2019; Hermans *et al.*, 2024), increased prey visibility (Evens *et al.*, 2023) or disruption of defence mechanisms (Wakefield *et al.*, 2015).

Moths are an interesting and emblematic group of study species when it comes to light pollution, as most species are nocturnal and adults are attracted to artificial light sources (van Langevelde *et al.*, 2018). Moths fulfil several ecological roles as herbivores, pollinators, hosts for parasitoids and food for other invertebrate and vertebrate predators, including bats (Corcoran & Conner, 2016) and birds (Evans *et al.*, 2024). The best-known effect of artificial light on moths is the typical flight-to-light response (e.g., Altermatt & Ebert, 2016). Nocturnal flying insects orientate by keeping the light source on their dorsal side (Fabian *et al.*, 2024). This works fine under natural night conditions with distant moon and starlight, but body orientation and, ultimately, flight performance is impaired by showing a similar response to nearby streetlights or other artificial light sources at night. Therefore, correct body orientation during flight is maintained under skyglow without local light sources (Fabian *et al.*, 2024). However, skyglow can mask the perception of celestial bodies (Falchi *et al.*, 2016) that are used for navigation in migrating moths (Sotthibandhu & Baker, 1979; Warrant *et al.*, 2024) and in other animal species (e.g., amphipods: Torres *et al.*, 2020 and birds: Horton *et al.*, 2023). In moths, ALAN effects go beyond flight disruption, as it may also disturb reproductive behaviour through reduced pheromone production (van Geffen *et al.*, 2015b) and mate calling (Cieraad *et al.*, 2022), adult feeding behaviour (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022), diapause induction (van Geffen *et al.*, 2014; Merckx *et al.*, 2023) and larval growth (van Geffen *et al.*, 2014; Grenis & Murphy, 2019).

Single-species studies provide insightful information on how individuals react to ALAN, but not all moth species respond in an equally strong way. Moth families have been shown to differ in their attraction to ALAN (Merckx & Slade, 2014). Species with a stronger flight-to-light response are more

distracted from essential behaviour such as adult feeding (Cieraad *et al.*, 2022) and mating (van Geffen *et al.*, 2015b). The way different species effects of ALAN cumulatively and interactively extend into community effects is still poorly understood. Community-based analyses can therefore provide novel ecological insights into ALAN-mediated filtering effects of species (Sanders & Gaston, 2018). In general, the number of studies addressing ALAN effects at the community level is still limited (Lacoeuilhe *et al.*, 2014; Bennie *et al.*, 2018; Bucher *et al.*, 2023; Cesarz *et al.*, 2023; Spoelstra *et al.*, 2023), including for moth communities (Grenis *et al.*, 2023; Sanetra *et al.*, 2024). Environmental stressors constrain the presence of species through selection on ecological traits (Belyea & Lancaster, 1999). Community-based studies shed light on differences in species composition under ALAN, but trait-based studies delve deeper into the mechanistic understanding of how and why such differences emerge by indicating which species traits are filtered out by environmental stressors such as light pollution (Zakharova *et al.*, 2019; Green *et al.*, 2022). Moreover, such an approach is likely to point at more generalizable global effects, independent of species identity (e.g., Belitz *et al.*, 2024). To the best of our knowledge, trait-based studies on the effects of ALAN have recently been done for very few species groups only (e.g., plants: Bucher *et al.*, 2023 and multi-taxon soil communities: Cesarz *et al.*, 2023), but not yet for moths. In NW-Europe, moth diversity and life-history traits are relatively well known (e.g., Franzén & Betzholtz, 2012; van Langevelde *et al.*, 2018; Maes *et al.*, 2024), which renders them suitable for such an approach.

Research on the ecological impact of skyglow is still in its infancy. Realistic skyglow-like conditions are hard to simulate under lab settings. Moth studies using direct artificial light sources at dim intensities usually still reach light levels one order of magnitude stronger than typical skyglow conditions (Cieraad *et al.*, 2022; van Geffen *et al.*, 2014; but see Merckx *et al.*, 2023). The only two community-based studies on moths that included ambient skyglow in their analysis were restricted to a single urban area. In a German study (Sanetra *et al.*, 2024), skyglow levels were highly correlated with urbanisation, which makes it difficult to separate both effects. An American study (Grenis *et al.*, 2023) sampled moth communities on prairie sites that were all located in highly urbanised environments with high to very high skyglow levels. The latter study also included ambient light intensity in their analyses (Grenis *et al.*, 2023), but in a highly urbanised context, its effect is again difficult to disentangle from other factors linked to urbanisation. Therefore, there is scope for a study design that simultaneously decouples light pollution levels from urbanisation levels and keeps urbanisation levels as low as possible. Moreover, such a study design allows for the much-needed testing of additive, or potentially interactive, effects of skyglow and

direct light pollution. Here, we adopted a two-level study design for ALAN effects in regions with low-medium and high-medium skyglow to investigate whether both skyglow and direct light pollution by streetlights affect moth communities. While the negative impact of direct light pollution on moths mainly comes from flight-to-light effects in adults and from increased mortality or sub-lethal effects during development at a local scale (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Fabian *et al.*, 2024), skyglow is expected to put more chronic and region-wide pressure on larval development and hence adult production (Merckx *et al.*, 2023). To test the hypothesis that both types of ALAN act as filters for morphology, behaviour and life-history traits, we performed trait-based analyses using a community-weighted mean approach. As light intensity from streetlights is around two orders of magnitude stronger than light pollution from skyglow, we expect the impact of direct light pollution on moth communities to be more important compared to skyglow, but our study also tested whether the effects of streetlights are weaker under high-medium skyglow.

Methods

Study areas and data on skyglow and direct light pollution by streetlights

We used a full-factorial design of skyglow and direct light pollution to analyse moth communities. To do so, two regions that differed significantly in average skyglow intensity were selected; in Southern Belgium skyglow levels are low-medium (Sky Quality Meter (SQM; lower value = higher skyglow level): 20.82–21.36 mag./arc sec²), while in Central Belgium they are high-medium (SQM: 19.50–20.55 mag./arc sec²) (data from <http://www.lightpollutionmap.info>; Falchi *et al.*, 2016). In both regions, twelve gardens were selected as study sites (Fig. S6.1, Appendix C6). Gardens are private land with variable impact of incoming streetlight, which render them highly suitable for our study. In each garden, moths were trapped in two consecutive years at a pre-designated trapping site. Gardens with the trapping site less than 30 m away from a streetlight were considered as ‘illuminated’ (n = 6 and n = 5 under low-medium and high-medium skyglow, respectively). The other gardens were considered as ‘dark’ (n = 6 and n = 7 under low-medium and high-medium skyglow, respectively). In illuminated gardens, streetlight was never blocked by obstacles (e.g., trees and fences), whereas in dark gardens, streetlight was at least partially blocked, especially when the trapping site was only a little further than 30 m away from the streetlight. Besides the presence/absence of streetlights, gardens were judged on the presence of potential host and nectar plants for moths. All

gardens contained a variety of indigenous trees and shrubs combined with herbaceous vegetation with low mowing intensity. In the second year of sampling, one garden in both regions was replaced by a different garden nearby with similar light and environmental conditions. To ensure that the effects of ALAN could be distinguished from those of climate and urbanization, different environmental variables were measured at each trapping site (Table S6.1, Appendix C6): (i) dataloggers (HOBO U23 Pro v2; ± 0.2 °C from 0 to 70 °C; ± 2.5 % between 10 and 90 % and ± 5 % below 10 and over 90 %; Onset Computer Corporation) were placed at a height of 40 cm to continuously record temperature and relative humidity; (ii) garden area was measured in QGIS 3.8; (iii) within a 400-m radius around the trapping site, the number of streetlights was counted and the proportion of built-up and forested area was calculated.

Moth sampling: light traps and bait traps

Our study could rely on the help of a careful selection of garden owners who contributed as citizen scientists providing data on moths based on strict guidelines from, and consultation with our team. Moth communities were sampled by the owners of the selected gardens using light and bait traps. Light traps (LedTrap, Dutch Butterfly Conservation) had a 5050 UV LED strip⁸ (peak wavelength: 410 nm). This light trap type is c. four times more effective than the commonly used Heath trap (6 W actinic) and is powered in an energy-efficient way by a simple powerbank (van Deijk *et al.*, 2024). As the attraction range of this trap type is quite low (c. 25 m), they are well-suited for local sampling of moths under environmental conditions that can vary at a small spatial scale. Traps were filled with egg cartons to provide hiding places for the moths. Each garden was sampled during two nights in July 2021 and three nights in September 2021, June and August 2022 (final number of light trap nights for: low-medium skyglow + dark – 69; low-medium skyglow + illuminated – 65; high-medium skyglow + dark – 56; high-medium skyglow + illuminated – 75). Light traps were automatically activated at sunset and emptied within one hour after sunrise. One light trap night corresponds to a single light trap emptied after a single night of activity. All individual moths, including all moth families of both the macro- and micro-moths, were photographed by the garden owners. Pictures were sent to us and moths were identified using Sterling *et al.* (2012) and Waring *et al.* (2015).

Light traps are often considered to be less efficient under light-polluted conditions (Yela & Holyoak, 1997). To verify the robustness of the light trap results in terms of moth abundance and species richness, Jalas bait traps

⁸ Epistar

(www.viestipaino.fi/rysa.html) were hung in a tree or shrub at 3 m away from the light trap, with the opening at a height of c. 1 m. Bait traps are considered to be light-insensitive (Yela & Holyoak, 1997). They were continuously active during the same months as the light traps, except in June 2022. A mixture of wine and sugar (1 kg/L; 350 mL/trap) was used as attractant and chloroform (150 mL/trap) as killing agent. These substances were refilled after 9–14 days (2021: July1: 10 days, July2: 9 days, September: 12 days; 2022: August1: 14 days, August2: 13 days), and moths were retrieved and stored in a freezer (–18 °C) until identification. One bait trap sample corresponds to a single bait trap emptied during a bait refill. Specimens that were no longer identifiable by wing characteristics were identified by checking dissected genitalia under a stereomicroscope (Viking n° 760070, 10–20 x + Euromex NexiusZoom EVO, 6.5–55 x).

For each light trap night and bait trap sample, moth abundance, species richness, Shannon diversity and Shannon evenness were calculated.

Moth species life history and morphological traits

Based on their potential sensitivity for light pollution, the following moth species life-history and morphological traits were selected: forewing length, voltinism, habitat structure, hibernating stage, larval habitation⁹, larval food specificity and adult activity peak (see Table 6.1 for summary of traits).

⁹ Place on the food source where the larva feeds.

Table 6.1. Species traits – Description of the species life-history and morphological traits and the sources used for data collection.

Species trait	Trait value(s)	Description	Source(s)
Body size	Forewing length	Continuous (mm)	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015)
Voltinism	Monovoltine Bivoltine Multivoltine	Binary 1: Monovoltine 0: Bi-/Multivoltine	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015) De Prins & Steeman (2003)
Larval food specificity	Monophagous Oligophagous Polyphagous	Binary 1: Monophagous 0: Oligo-/ Polyphagous	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015)
Habitat structure	Generalist Closed habitat Open habitat	Binary All trait values were tested separately	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015)
Hibernating stage	Egg Larva Pupa Adult	Binary 1: Larva 0: Other stages	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015)
Larval habitation	Open on food plant Hidden in food plant or in rolled-up leaf Leaf mine Underground	Binary 1: Hidden in food plant or in rolled-up leaf 0: Other	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015) De Prins & Steeman (2003)
Adult activity peak	Diurnal Crepuscular Nocturnal	Binary 1: Crepuscular 0: Other	Sterling <i>et al.</i> (2012) Waring <i>et al.</i> (2015)

Statistical analyses

First, differences in environmental conditions were tested with a multi-way between-group ANOVA. For light and bait traps separately, we tested for differences in moth abundance and species richness between skyglow and streetlight conditions as well as their interaction, using generalized linear mixed models (GLMM) with a Poisson error distribution. Linear mixed models (LMM) were used to test for differences in Shannon diversity and evenness. Differences in community composition were tested with a perMANOVA test with a Chord-distance matrix based on species abundance using the *adonis2*-function in the R package *vegan*. This was done for pooled communities for light and bait traps separately. Non-metric multidimensional scaling (NMDS) with Chord distance was used for visualisation of variation in community composition. For the light trap samples, community weighted means (CWM) of each species trait were calculated based on presence-absence data. CWM

thus refer to the relative frequency of species traits (i.e., the number of species with a certain trait weighted relative to the number of species present in the local community). We tested for differences in CWM between skyglow and streetlight conditions as well as their interaction, using LMM models. For all GLMM and LMM models, mean night temperature (mean over all nights in a sample period for bait traps) was included as a covariate and day (first day of sample period for bait traps), year and garden location were included as random variables. Relative humidity was left out of the analyses due to significant negative correlation with temperature and low precision near saturation (above 90 %). Since four of trapping sites (one under low-medium and three under high-medium skyglow) were located near our threshold of 30 m from the nearest streetlight, we additionally performed the same analyses with these four sites removed. The effects are shown in Appendix C6 (Table S6.2-4; Fig. S6.5-6.9) and are qualitatively similar to our full analysis, thus supporting our study design based on the 30-m threshold. All analyses were performed in R 4.3.3 (R Development Core Team, 2024). In the results section, we adopted the language of evidence (Muff *et al.*, 2022).

Results

Environmental conditions

Temperature was significantly higher in gardens under high-medium skyglow (+1.7 °C) and near streetlights (+1.1 °C). Relative humidity was significantly lower near streetlights (−2.9 %). However, the treatment groups did not differ in the amount of built-up area (400 m radius), the number of streetlights (400 m radius), the amount of forested area (400 m radius) and garden surface area (Table S6.1, Appendix C6).

Moth abundance and species richness relative to direct and indirect light pollution

Captured moths by trap method

In 265 individual light trap nights, we observed 10473 moth specimens of 543 species. In all 24 gardens, the bait traps were active over 58 nights. This yielded 6 230 moth specimens of 192 species. Both trap types had 143 species in common; Sørensen similarity between both trap types was 0.38 and Bray-Curtis similarity was 0.24, suggesting there was only weak overlap

between trapping methods. The number of overlapping species between light conditions is shown in Fig. S6.2 (Appendix C6).

Moth abundance

In the light traps, moth abundance ranged from 1 to 319 (mean $\pm$ SE: 40 $\pm$ 2) moths/light trap night. There was no evidence for skyglow effects on abundance and very strong evidence for a 41.7 % lower abundance in illuminated gardens (Fig. 6.1A; Table 6.2). The bait traps yielded 1 to 459 (mean $\pm$ SE: 50 $\pm$ 6) moths/bait trap sample. We found some evidence for a 70.9 % lower abundance under high-medium skyglow and very strong evidence for a 69.4 % lower abundance in illuminated gardens (Fig. 6.1B; Table 6.2).

Moth species richness

For the light traps, moth species richness ranged from 1 to 68 (mean $\pm$ SE: 18 $\pm$ 1) species/light trap night. We found no evidence for an effect of skyglow on species richness and strong evidence for 27.8 % lower species richness in gardens illuminated by streetlights (Fig. 6.1C; Table 6.2), but this was mainly due to the strong correlation with moth abundance ($\chi^2 = 191.90$, $p < 0.001$). In the bait traps, 1 to 44 (mean $\pm$ SE: 12 $\pm$ 1) moth species/bait trap sample were caught. We found no evidence for an effect of skyglow on species richness and strong evidence for 42.2 % lower species richness in illuminated gardens (Fig. 6.1D; Table 6.2). However, also here a positive abundance effect was the main driver ($\chi^2 = 73.70$, $p < 0.001$).

Moth diversity and evenness

For the light traps, we found no evidence for an effect of skyglow on Shannon diversity and some evidence for lower diversity in gardens illuminated by streetlights (Fig. 6.1E; Table 6.2). We found no evidence for effects of skyglow and streetlight pollution on evenness of the moth community (Fig. 6.1G; Table 6.2). In the bait traps, we found no evidence for an effect of skyglow on Shannon diversity and weak evidence for lower diversity in illuminated gardens (Fig. 6.1F; Table 6.2). We found no evidence for skyglow effects on evenness, but some evidence for higher evenness in gardens illuminated by streetlights (Fig. 6.1H; Table 6.2).

Table 6.2. Results moth diversity – Statistical output for differences in moth diversity in the light and bait traps. The interaction between skyglow and streetlights was non-significant and thus removed from our models. All tests are based on d.f. = 1. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

	Skyglow	Streetlight	Night temperature
Abundance			
- Light trap	$\chi^2 = 3.54, p = 0.102$	$\chi^2 = 11.58, p = 0.003$	$\chi^2 = 332.71, p < 0.001$
- Bait trap	$\chi^2 = 6.48, p = 0.029$	$\chi^2 = 11.57, p = 0.003$	$\chi^2 = 122.53, p < 0.001$
Species richness			
- Light trap	$\chi^2 = 1.50, p = 0.312$	$\chi^2 = 8.62, p = 0.011$	$\chi^2 = 81.86, p < 0.001$
- Bait trap	$\chi^2 = 1.95, p = 0.243$	$\chi^2 = 8.26, p = 0.012$	$\chi^2 = 4.03, p = 0.089^\circ$
Shannon diversity			
- Light trap	$\chi^2 = 0.94, p = 0.387$	$\chi^2 = 5.42, p = 0.043$	$\chi^2 = 34.31, p < 0.001$
- Bait trap	$\chi^2 = 0.01, p = 0.941$	$\chi^2 = 3.76, p = 0.097^\circ$	$\chi^2 = 0.35, p = 0.603$
Shannon evenness			
- Light trap	$\chi^2 = 0.91, p = 0.388$	$\chi^2 = 1.08, p = 0.388$	$\chi^2 = 0.98, p = 0.388$
- Bait trap	$\chi^2 = 3.11, p = 0.125$	$\chi^2 = 5.68, p = 0.041$	$\chi^2 = 0.04, p = 0.872$

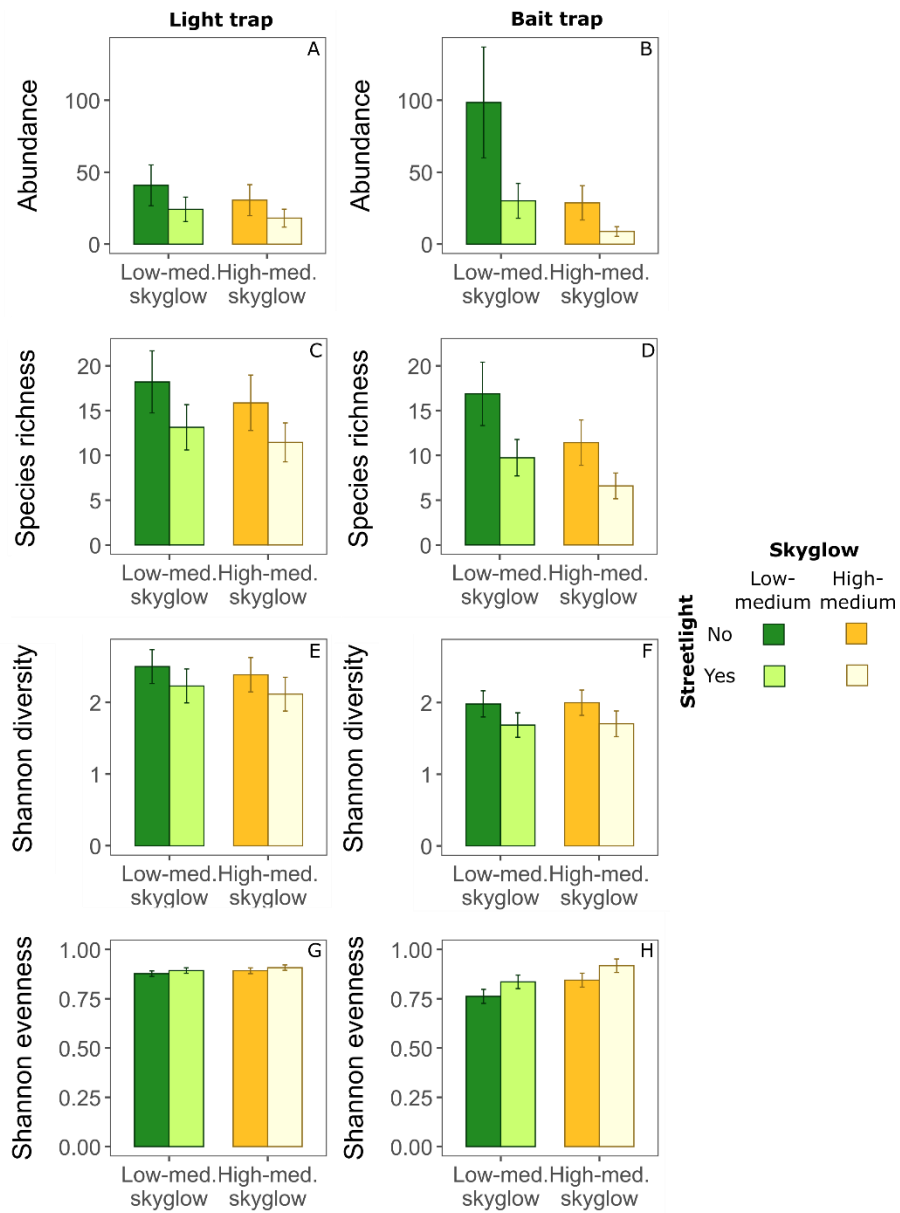


Fig. 6.1. Moth diversity – Model parameter estimates $\pm$ SE of moth abundance, species richness, Shannon diversity and Shannon evenness under the sampled skyglow and streetlight conditions for (A,C,E,G) light traps and (B,D,F,H) bait traps.

Moth community composition relative to direct and indirect light pollution

Moth community composition was different for light traps compared to bait traps ($F_{1,50} = 20.03$, $p < 0.001$). For the light traps, we found strong evidence for an effect of skyglow ($F_{1,22} = 3.96$, $p < 0.001$) and of streetlights ($F_{1,22} = 2.38$, $p = 0.002$) on community composition. In general, more species of Noctuidae were found at a higher abundance at low-medium skyglow levels, while the opposite is the case for Tortricidae (Fig. S6.3A-B, Appendix C6). Crambidae species are more often found in illuminated gardens (Fig. S6.3C, Appendix C6), and Geometridae are more evenly spread over the four light conditions (Fig. S6.3D, Appendix C6). In the bait traps, we found strong evidence for an effect of skyglow ($F_{1,22} = 4.20$, $p = 0.001$) and weaker evidence for streetlight effects ($F_{1,22} = 1.78$, $p = 0.058$) on community composition. Bait trap communities mainly consisted of Noctuidae, but there was no clear pattern over the different light conditions (Fig. S6.4, Appendix C6). A quarter of all the moth species captured in the bait traps were only found in gardens without skyglow and streetlights and not in any of the other conditions (Fig. S6.2B, Appendix C6).

Moth species traits under direct and indirect light pollution: a community weighted means approach

We found no evidence for effects of skyglow and direct light pollution on average moth species size measured by forewing length (Fig. 6.2A). Moth communities in illuminated gardens had more monovoltine species than dark gardens (moderate evidence) (Fig. 6.2B; Table 6.3). Moth communities in illuminated gardens had more monophagous species than dark gardens (moderate evidence) (Fig. 6.2C). We found some evidence for fewer habitat generalists in moth communities in illuminated gardens, while the opposite was true for species of open habitats (very strong evidence) (Fig. 6.2D-F; Table 6.3). We found strong evidence for moth communities in gardens under high-medium skyglow or in illuminated gardens having more species that hibernate in the larval stage (Fig. 6.2G). Moth communities in gardens under high-medium skyglow had more species whose larvae live hidden in the food plant or in a rolled-up leaf (moderate evidence) (Fig. 6.2H). We found no evidence for effects of skyglow and streetlight pollution on the presence of twilight active species (Fig. 6.2I; Table 6.3).

Table 6.3. Results trait community weighted means – Statistical output for differences in trait community weighted means in the light traps. The interaction between skyglow and streetlights was non-significant and thus removed from our models. All tests are based on d.f. = 1. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

	Skyglow	Streetlight	Night temperature
Forewing length	$\chi^2 = 0.06, p = 0.869$	$\chi^2 = 0.32, p = 0.673$	$\chi^2 = \mathbf{11.41}, p = \mathbf{0.009}$
Monovoltine	$\chi^2 = 0.85, p = 0.621$	$\chi^2 = 6.05, p = 0.051^\circ$	$\chi^2 = 1.24, p = 0.221$
Larva monophagous	$\chi^2 = 1.38, p = 0.621$	$\chi^2 = 4.72, p = 0.059^\circ$	$\chi^2 = \mathbf{15.19}, p = \mathbf{0.035}$
Habitat generalist	$\chi^2 = 1.16, p = 0.448$	$\chi^2 = \mathbf{6.78}, p = \mathbf{0.035}$	$\chi^2 = 3.27, p = 0.147$
Open habitats	$\chi^2 = 0.02, p = 0.888$	$\chi^2 = \mathbf{18.66}, p < \mathbf{0.001}$	$\chi^2 = 0.47, p = 0.635$
Closed habitats	$\chi^2 = 1.64, p = 0.339$	$\chi^2 = 0.56, p = 0.621$	$\chi^2 = \mathbf{6.49}, p = \mathbf{0.037}$
Larval hibernation	$\chi^2 = \mathbf{8.40}, p = \mathbf{0.032}$	$\chi^2 = \mathbf{7.94}, p = \mathbf{0.032}$	$\chi^2 = 0.03, p = 0.887$
Larva hidden in food plant or in rolled-up leaf	$\chi^2 = \mathbf{6.21}, p = \mathbf{0.032}$	$\chi^2 = 1.45, p = 0.146$	$\chi^2 = 0.07, p = 0.852$
Adult crepuscular	$\chi^2 = 0.32, p = 0.673$	$\chi^2 = 2.63, p = 0.203$	$\chi^2 = 4.02, p = 0.110$

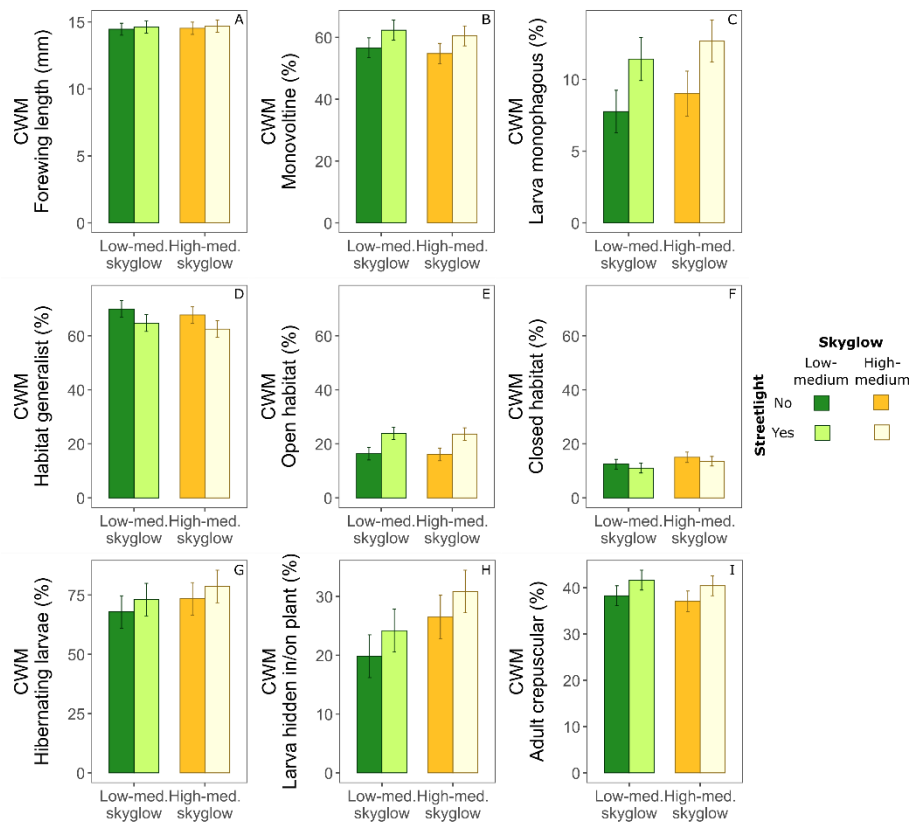


Fig. 6.2. Trait community weighted means – Model parameter estimates $\pm$ SE for community-weighted means of the tested morphological, behavioural and life-history traits under the sampled skyglow and streetlight conditions. Only moths captured with light traps were included.

Discussion

Our results provide evidence for multiple significant alterations in garden moth communities relative to both indirect light pollution by skyglow and direct light pollution by nearby streetlights. Streetlight effects occurred more often and were usually stronger than skyglow effects. Moth abundance decreased with higher skyglow and direct streetlight pollution, and species richness and diversity were lower under direct light pollution. Community composition changed as well due to skyglow and streetlights. These latter ALAN-related effects on the local moth communities were reflected in differences in morphological, behavioural and life-history traits of the species. We discuss the mechanisms that could have led to the reduction of

moth numbers under ALAN and potential consequences for the ecosystem, how the results on species traits can be explained in a context of light pollution and we consider perspectives for future studies.

We showed negative effects of both skyglow and streetlights on moth abundance, while species richness was only affected by streetlights. Overall, the observed effects were quantitatively similar for the datasets of light and bait traps, respectively, indicating that our light trap catches were robust, even though earlier work claimed that their efficiency is negatively affected by ambient light at night (Yela & Holyoak, 1997). Grenis *et al.* (2023) showed a similar negative effect of skyglow on moth abundance, but a positive effect of direct light pollution on moth abundance and species richness on locations with medium to very high skyglow levels (measured SQM: 11.20–19.99 mag./arc sec², www.lightpollutionmap.info: 18.90–20.00 mag./arc sec²). Such high skyglow levels could, however, hide the impact from other light sources (Dickerson *et al.*, 2022). In turn, in the study of Sanetra *et al.* (2024) with medium-high skyglow levels at a smaller range compared to our study (19.20–20.64 mag./arc sec²), there was no effect of skyglow on moth abundance or species richness. However, it should be noted that effects of light pollution are unlikely to be separated from other urbanisation effects *per se* (e.g., Vähätalo *et al.*, 2024) in both these studies. In our study design, variation in light pollution was largely independent of urbanisation (Table S6.1, Appendix C6). Our study could not control for all potential regional differences between Central and Southern Belgium (e.g., topography, altitude and plant communities) that could also contribute, alongside light pollution, to variations in moth communities. However, there is growing support for dominant effects of light pollution on moths (e.g., Boyes *et al.*, 2021), although a careful further analysis of overruling *versus* synergetic effects of light pollution and other ecological factors is warranted.

Because the effects of skyglow and direct light pollution play at different spatial scales, the mechanisms by which they lead to a reduction in moth numbers are likely to be different. Skyglow spreads over a broader spatial scale (i.e., kilometres) making it plausible that the lower moth numbers under high-medium skyglow are not limited to the sampling site, but result from a regional scale effect. Skyglow can impose chronic stress on larval development by disturbing growth and diapause inhibition (Merckx *et al.*, 2023). Lower body mass can lead to lower fecundity, particularly in females (Lamunyon, 1997; Garrad *et al.*, 2016). ALAN-related disruption of winter diapause would result in increased mortality, which in turn could contribute to local population declines. In the case of no demographic compensation by immigration from dark-sky populations, this will reinforce low moth abundance. For lower moth numbers near streetlights, two potential mechanisms are conceivable. By attracting moths and accumulating moth

numbers, streetlights may induce a local concentration effect for moth abundance. However, such a streetlight concentration effect may lead to increased mortality due to predation facilitation or to exhaustion after circling around the light (Eisenbeis & Hänel, 2009), leading ultimately to a net loss of moths. Although it has been observed previously that species vary in their attraction to artificial light at the adult stage (Somers-Yeates *et al.*, 2013; Merckx & Slade, 2014), direct light pollution may also affect local moth communities in different ways through larval effects including body mass reduction (Grenis & Murphy, 2019) and diapause inhibition (van Geffen *et al.*, 2014). In a similar way as for skyglow, this can also lead to reduced moth abundances. Secondly, moths could be locally attracted by the nearby streetlight, drawing them away from nearby parts of the garden (i.e., vacuum cleaner effect: Eisenbeis & Hänel, 2009). Local moth numbers are then not necessarily lower, but there would be stronger fine-scale heterogeneity in moth occurrence. Both mechanisms are not necessarily mutually exclusive and may hence be both at play simultaneously.

Through the lens of trophic interactions between moths and their predators, indicators of local and regional moth biomass are of high relevance, independent of species identity (e.g., Dey & Balakrishnan, 2024). The available food mass relates to the combination of moth size and abundance. Community body size (i.e., average forewing length) was not affected by light pollution. When average body size remains stable, moth biomass is determined by the number of moths. The reduced moth abundance under skyglow and direct light pollution therefore leads to a decrease in biomass. This corresponds to lower food availability for various invertebrate parasites and predators (Kuhlmann *et al.*, 1998), bats (Corcoran & Conner, 2016) and birds (Evans *et al.*, 2024).

Worldwide, pollinators show strong declines (Potts *et al.*, 2010; IPBES, 2016) and the functional significance of nocturnal pollinators has been underappreciated (Macgregor & Scott-Brown, 2020). Moths are an important part of the nocturnal pollination network and can even achieve higher pollination rates than diurnal pollinators, not only in moth-specialised plants (Macgregor *et al.*, 2019), but also in common plants such as bramble *Rubus* sp. (Anderson *et al.*, 2023). A study on pollination of strawberries showed a positive additive effect on fruit quality under conditions of both diurnal and nocturnal pollination (Fijen *et al.*, 2023). Consequently, a decline in moth numbers could jeopardise a significant proportion of pollination and hence plant reproduction (Macgregor *et al.*, 2019; Alison *et al.*, 2022). More work in line with the study of Macgregor *et al.* (2019) is warranted to investigate whether light pollution affects nocturnal flower visitation and whether this affects pollination rate and seed or fruit quality, both in plants specialised in nocturnal pollination and in plants that are pollinated both

during the day and at night. It is relevant for gardens, but obviously also for other environments with cultivated, ornamental and wild insect-pollinated plant species.

Not only moths, but also their host plants are potentially affected by light pollution. ALAN has been shown to affect plant phenology (Bennie *et al.*, 2018), biomass and functional traits (Murphy *et al.*, 2022; Bucher *et al.*, 2023), leading to changes in plant communities (Bucher *et al.*, 2023). When larval food plants are affected by light pollution, polyphagous species could be expected to have an advantage over monophagous species as they can switch to other food plants (e.g., Belitz *et al.*, 2024). However, monophagous species showed a relatively higher incidence in gardens that are illuminated by streetlights. This unexpected result is partly driven by the increased incidence of monophagous species like *Pyrausta despicata* (Crambidae) and *Celypha striana* (Tortricidae) that feed on *Plantago* sp. and *Taraxacum* sp., respectively. However, the main driver is the lower incidence of species that are very common herbaceous plant generalists, such as *Diarsia rubi*, *Xestia xanthographa* (Noctuidae) and *Celypha lacunana* (Tortricidae). The mechanism behind this result remains obscure and requires further investigation.

Monovoltine moth species experience on average stronger population declines than multivoltine species (Potocký *et al.*, 2018; Tordoff *et al.*, 2022; but see Maes *et al.*, 2024). Monovoltine species are usually less flexible to changes in phenology (e.g., due to climatic variation: Valtonen *et al.*, 2017). Light pollution has the potential to affect moth phenology by accelerating larval development (van Geffen *et al.*, 2014) and disrupting diapause (van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Merckx *et al.*, 2023). Therefore, one could expect lower incidence of monovoltine species under light pollution. However, results of a Finnish study showed that moth phenology is influenced by differences in temperature rather than by ALAN (Merckx *et al.*, 2021), which may explain why we did not find less monovoltine species.

In a context of urbanization and moth communities, habitat specialists are usually replaced by habitat generalists (Merckx & Van Dyck, 2019; Franzén *et al.*, 2020; Sanetra *et al.*, 2024). However, in our study we did not quantify habitat specialism, but species were assigned to their preferred habitat structure type (i.e., open, closed or both). Moth species with a preference for an open habitat structure occurred relatively more frequently in illuminated gardens. This result was mainly driven by the reduced occurrence of species present in both open and closed habitats, while the presence of common species of open habitats (e.g., *Agriphila* sp., *Chrysoteuchia culmella* (Crambidae), *Mythimna albipuncta* (Noctuidae) and *Spilosoma lubricipeda* (Erebidae)) was equal to or higher than in dark gardens. All these species can be seen as open-habitat generalists, as they occur in a wide variety of open

habitats (Waring *et al.*, 2015). The listed Crambidae species are at least partially diurnal, which could make them less sensitive to ALAN (van Langevelde *et al.*, 2018), but for the other, nocturnal, species, potential mechanisms remain unclear for now. The proportion of closed-habitat species was generally low and remained more or less the same across all light pollution conditions. Due to the large area they occupy (e.g., 8 % in the northern part of Belgium: Dewaelheyns *et al.*, 2014), gardens have great potential to enhance biodiversity in residential areas (Delahay *et al.*, 2023; Timberlake *et al.*, 2024). However, in this region gardens consist mainly of open habitat and thus are more likely to positively affect open habitat species or habitat generalists than forest species.

Through feeding, larvae build up the resource capital and body size of the adult stage. We did not have data on capital *versus* income breeding of the moth species in the garden communities (e.g., Javoiš *et al.*, 2011). Unless larval feeding is significantly perturbed by light pollution, income breeding moth species are predicted to be more heavily impacted by ALAN than capital breeders. However, this will be conditional on the proportion of flower resources that occur under illuminated conditions. To some extent, tree cover could mitigate direct light pollution effects (e.g., Majewska & Altizer, 2020; Straka *et al.*, 2021). In their meta-analysis, Majewska and Altizer (2020) pointed at the strong relevance of within-garden features for pollinators, sometimes even overruling surrounding landscape factors. Moth species that hibernate as larvae occurred more frequently under higher skyglow and streetlight pollution. This result is, however, counterintuitive, as the induction of larval and pupal diapause is usually determined during the larval stages (Numata & Shintani, 2023) and it has been shown in different moth families that ALAN has the potential to inhibit this induction (van Geffen *et al.*, 2014; Merckx *et al.*, 2023). However, while the decision for pupal diapause inhibition is probably final once the pupal stage is reached, this may be reversible for larval diapause as diapause is also influenced by temperature (e.g., Xu *et al.*, 2014) or nutrition (Short & Hahn, 2023). This potentially renders species with pupal diapause more vulnerable to light pollution than species with larval diapause. Interestingly, species with larvae that live hidden in the food plant or between leaves occurred more frequently under high-medium skyglow conditions. This result suggests that plant material can act as a buffer against ambient ALAN. Indeed, larvae living hidden in or between plant material experience much lower light levels than larvae living open on their foodplant (Summers *et al.*, 2024), which could mitigate some ALAN effects in these species. However, this does not mean that they escape from negative effects as even low light levels can already affect their behaviour (Summers *et al.*, 2024).

Most studies on moth communities (e.g., Merckx & Van Dyck, 2019; Grenis *et al.*, 2023; Sanetra *et al.*, 2024) and on species traits (e.g., van Langevelde *et al.*, 2018; Maes *et al.*, 2024) only included macro-moths in their analyses, often for practical reasons (Belitz *et al.*, 2024). However, we argue that micro-moths should not be ignored in moth studies. First of all, the traditional distinction between macro- and micro-moths is somewhat artificial, based solely on the size of most species within these clusters of moth families. Micro-moths represent a significant part of the moth fauna. In our samples, 41 % of the species and 24 % of the specimens were micro-moths. Moreover, micro-moths are likely to be more sensitive to small environmental changes than the macro-moths (Uhl *et al.*, 2022), although there is some overlap in body size. In any case, the inclusion of micro-moths broadens the range of morphological, behavioural and life history traits and hence offered us a more complete picture of the moth community under ALAN conditions.

Our study showed that both skyglow and direct light pollution from streetlights affect moth communities and both sources of ALAN act as filters for variation in species traits. This is a relevant proof of principle in the global change context of light pollution. It is now warranted to set up a follow-up study similar to ours but with multiple regional replicates for different skyglow levels, also including sites with truly dark skies, as this was not possible in our study area. Moreover, since clouds can drastically amplify skyglow levels (Kyba *et al.*, 2011), it is arguably useful to include cloud cover data in this kind of studies, especially when it is hard to obtain direct measurements of skyglow for each trapping night. Further, a study design in which moth communities are sampled at different distances from streetlights would also be a useful extension. A recent study (Degen *et al.*, 2024) actually showed that adult moth behaviour is influenced beyond the illuminated area of streetlights, and only a low percentage of moths showed the typical flight-to-light response. This result supports that ALAN effects on moths should not be studied with light traps alone, but combined with at least one other method (Jones & McNamara, 2024), as we did in our study.

Artificial light at night is a complex and intrusive global change issue that is associated with other ecological problems, including urbanisation and road infrastructure. In previous study designs, indirect light pollution by skyglow and direct light pollution by streetlights were often strongly correlated with urbanisation and both types of ALAN were rarely considered in an additive way. Using a two-level design of ALAN in gardens surrounded by landscapes with similar levels of urbanisation, we showed that both types of light pollution negatively affect garden moth communities. In addition, to the best of our knowledge, our study is the first to show light-pollution related filter effects of both skyglow and streetlights on species traits. Our results suggest

that locally reducing direct light pollution would only partially help restoring moth communities and regional-scale measures to reduce skyglow are required as well. Our study helps to underpin the much-needed integration of darkness quality within green and blue infrastructures for biodiversity in anthropogenic areas (Sordello *et al.*, 2022).

Data availability

All data and R code used for the analyses are available from Dryad Digital Repository: <https://doi.org/10.5061/dryad.6djh9w1d2>.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2025.126068> (Van de Schoot *et al.*, 2025b: Chapter 6).

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CRedit authorsip contribution statement

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

Methodological reflections

In *subsection 7.6.3 of Chapter 7*, we discuss a couple of methodological choices made in this chapter.

Appendix C6. Supplementary Information for 6. Skyglow and especially direct streetlight pollution alter moth communities

Authors: Evert Van de Schoot, Renate A. Wesselingh and Hans Van Dyck

Table S6.1. Range, mean and statistical output for multi-way between-group ANOVA's to test for environmental differences on sampling sites under different skyglow and streetlight conditions. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold.

	Skyglow		Streetlight	
	Low-medium	High-medium	No	Yes
SQM (mag./arc sec ²)	20.82-21.36 21.12 F_{1,23} = 106.06, p < 0.001	19.5-20.55 20.04	19.75-21.30 20.68 F _{1,23} = 0.01, p = 0.990	19.50-21.36 20.50
Distance to nearest streetlight (m)	11.65-75.49 35.42 F _{1,23} = 2.64, p = 0.274	9.41-164.43 42.70	34.07-164.43 67.00 F_{1,23} = 31.72, p < 0.001	9.41-27.14 15.11
Night temperature (°C)	6.19-23.31 13.18 F_{1,23} = 50.72, p < 0.001	7.00-21.44 14.85	6.19-22.21 13.44 F_{1,23} = 17.10, p < 0.001	7.90-23.31 14.51
Night relative humidity (%)	50.94-100.00 86.54 F _{1,23} = 2.43, p = 0.274	47.65-100.00 88.07	47.65-100.00 88.91 F_{1,23} = 9.62, p = 0.006	50.16-100.00 85.89
Built-up area (400 m) (%)	1.97-9.80 4.47 F _{1,23} = 0.13, p = 0.887	0.54-14.42 5.14	0.54-10.94 4.33 F _{1,23} = 1.09, p = 0.539	1.79-14.42 5.21
Nr streetlights (400 m)	16-258 58 F _{1,23} = 0.96, p = 0.539	7-106 40	7-258 53 F _{1,23} = 0.71, p = 0.595	21-98 45
Garden area (are)	5.32-39.89 15.06 F _{1,23} = 1.96, p = 0.350	4.84-65.54 24.76	5.32-65.54 21.29 F _{1,23} = 0.14, p = 0.887	4.84-60.60 18.73
Forested area (400 m) (%)	0.00-67.21 28.41 F _{1,23} = 0.054, p = 0.936	0.00-94.64 31.03	0.00-62.52 29.58 F _{1,23} = 0.00, p = 0.990	3.11-94.64 29.84

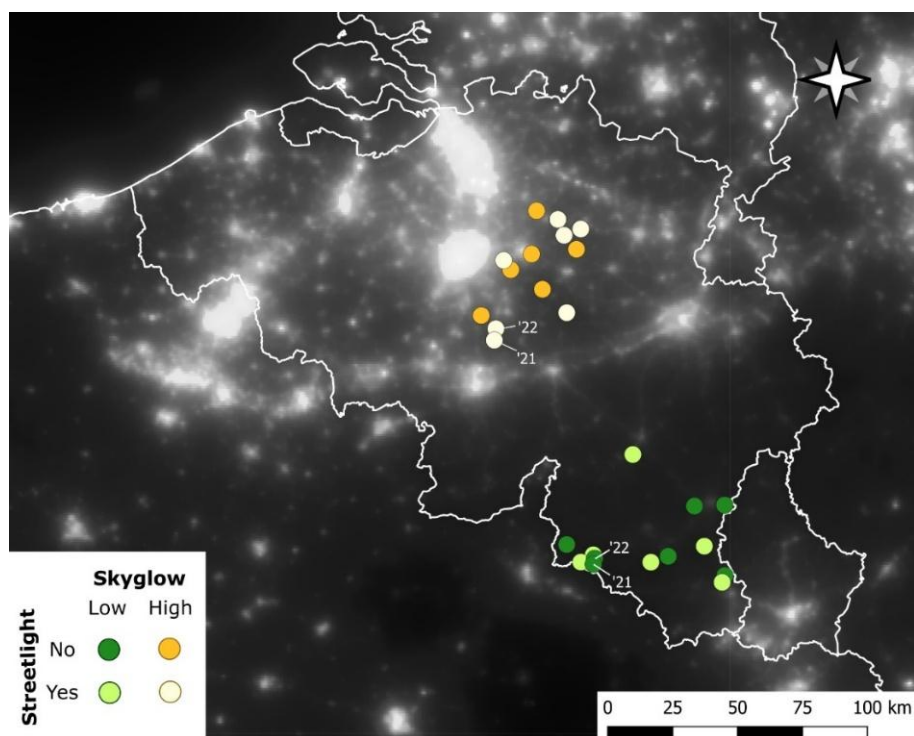


Fig. S6.1. Map of the sampling locations (green and yellow dots) with skyglow data retrieved from www.lightpollutionmap.info.

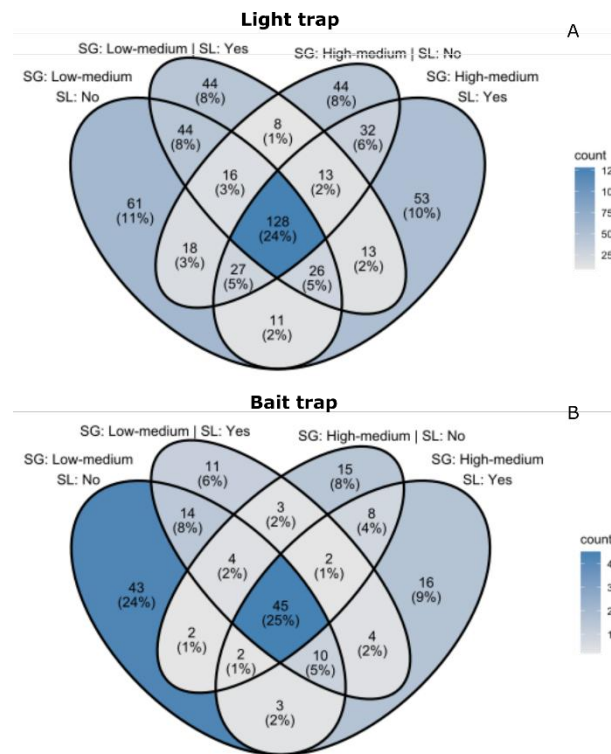


Fig. S6.2. Venn diagrams showing the number (and percentage) of shared species between the different light conditions for (A) light traps and (B) bait traps. SG = skyglow level; SL = streetlight presence.

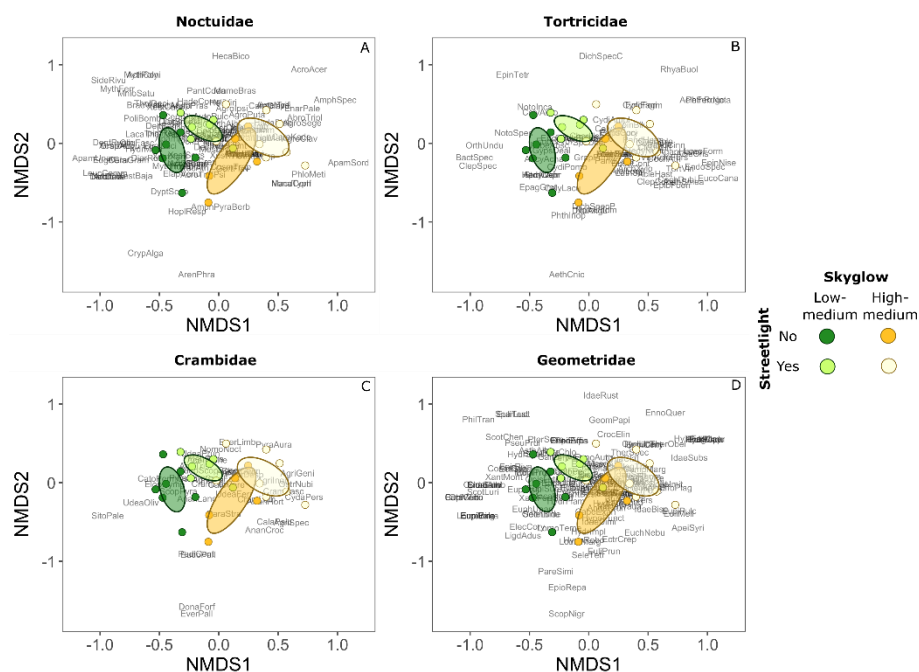


Fig. S6.3. Plot showing non-metric multidimensional scaling with Chord distance based on species abundance in light traps. Dots depict the sampling sites and ellipses show 95 % confidence intervals. Species scores are shown for (A) Noctuidae, (B) Tortricidae, (C) Crambidae and (D) Geometridae. Abbreviations of species names can be found in the dataset.

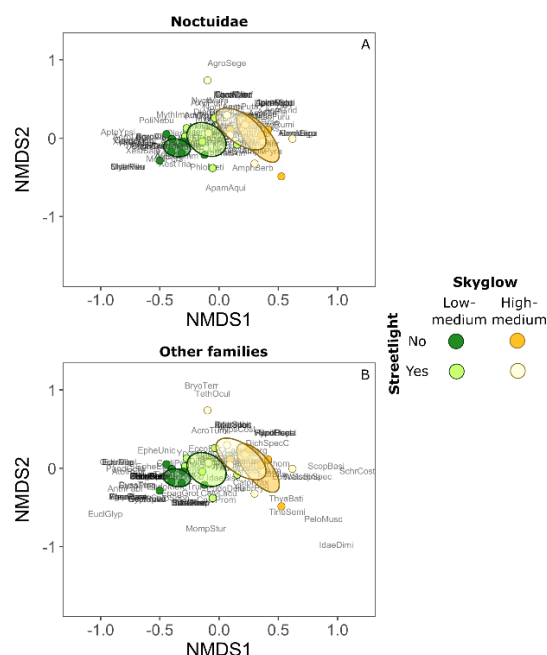


Fig. S6.4. Plot showing non-metric multidimensional scaling with Chord distance based on species abundance in bait traps. Dots depict the sampling sites and ellipses show 95 % confidence intervals. Species scores are shown for (A) Noctuidae and (B) the other moth families. Abbreviations of species names can be found in the dataset.

Analysis with four sampling sites removed

Table S6.2. Output for multi-way between-group ANOVA's to test for environmental differences on sampling sites under different skyglow and streetlight conditions; with 4 sampling sites removed. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold.

	Skyglow	Streetlight
SQM	$F_{1,23} = 95.37, p < 0.001$	$F_{1,23} = 0.22, p = 0.740$
Distance to nearest streetlight	$F_{1,23} = 2.67, p = 0.281$	$F_{1,23} = 31.97, p < 0.001$
Night temperature	$F_{1,23} = 27.64, p < 0.001$	$F_{1,23} = 18.32, p < 0.001$
Night relative humidity	$F_{1,23} = 2.39, p = 0.281$	$F_{1,23} = 5.79, p = 0.053^{\circ}$
Built-up area (400 m)	$F_{1,23} = 0.25, p = 0.740$	$F_{1,23} = 0.71, p = 0.605$
Nr streetlights (400 m)	$F_{1,23} = 1.05, p = 0.605$	$F_{1,23} = 0.82, p = 0.605$
Garden area	$F_{1,23} = 0.69, p = 0.605$	$F_{1,23} = 0.06, p = 0.870$
Forested area (400 m)	$F_{1,23} = 0.00, p = 0.961$	$F_{1,23} = 0.26, p = 0.740$

Table S6.3. Statistical output for differences in moth diversity in the light and bait traps; with 4 sampling sites removed. The interaction between skyglow and streetlights was non-significant and thus removed from our models. All tests are based on d.f. = 1. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

	Skyglow	Streetlight	Night temperature
Abundance			
- Light trap	$\chi^2 = 7.74$, p = 0.016	$\chi^2 = 8.97$, p = 0.009	$\chi^2 = 335.99$, p < 0.001
- Bait trap	$\chi^2 = 6.76$, p = 0.025	$\chi^2 = 12.72$, p = 0.002	$\chi^2 = 89.75$, p < 0.001
Species richness			
- Light trap	$\chi^2 = 2.81$, p = 0.155	$\chi^2 = 5.19$, p = 0.055°	$\chi^2 = 69.87$, p < 0.001
- Bait trap	$\chi^2 = 2.36$, p = 0.176	$\chi^2 = 8.98$, p = 0.009	$\chi^2 = 4.54$, p = 0.066°
Shannon diversity			
- Light trap	$\chi^2 = 1.43$, p = 0.309	$\chi^2 = 2.59$, p = 0.161	$\chi^2 = 25.16$, p < 0.001
- Bait trap	$\chi^2 = 0.01$, p = 0.913	$\chi^2 = 2.93$, p = 0.155	$\chi^2 = 0.60$, p = 0.479
Shannon evenness			
- Light trap	$\chi^2 = 1.05$, p = 0.386	$\chi^2 = 0.85$, p = 0.427	$\chi^2 = 0.37$, p = 0.569
- Bait trap	$\chi^2 = 2.76$, p = 0.155	$\chi^2 = 4.81$, p = 0.062°	$\chi^2 = 0.60$, p = 0.479

Table S6.4. Statistical output for differences in trait community weighted means in the light traps; with 4 sampling sites removed. The interaction between skyglow and streetlights was non-significant and thus removed from our models. All tests are based on d.f. = 1. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

	Skyglow	Streetlight	Night temperature
Forewing length	$\chi^2 = 0.34$, p = 0.774	$\chi^2 = 0.20$, p = 0.774	$\chi^2 = 5.66$, p = 0.099°
Monovoltine	$\chi^2 = 0.31$, p = 0.774	$\chi^2 = 2.92$, p = 0.182	$\chi^2 = 1.67$, p = 0.363
Larva monophagous	$\chi^2 = 0.32$, p = 0.774	$\chi^2 = 4.59$, p = 0.113	$\chi^2 = 4.52$, p = 0.113
Habitat generalist	$\chi^2 = 1.63$, p = 0.363	$\chi^2 = 4.24$, p = 0.118	$\chi^2 = 3.91$, p = 0.130
Open habitats	$\chi^2 = 0.09$, p = 0.832	$\chi^2 = 11.40$, p = 0.020	$\chi^2 = 0.02$, p = 0.927
Closed habitats	$\chi^2 = 0.97$, p = 0.515	$\chi^2 = 0.11$, p = 0.827	$\chi^2 = 5.55$, p = 0.100°
Larval hibernation	$\chi^2 = 6.35$, p = 0.100°	$\chi^2 = 4.70$, p = 0.113	$\chi^2 = 0.00$, p = 0.948
Larva hidden in food plant or in rolled-up leaf	$\chi^2 = 7.95$, p = 0.065°	$\chi^2 = 3.14$, p = 0.179	$\chi^2 = 0.19$, p = 0.774
Adult crepuscular	$\chi^2 = 0.22$, p = 0.774	$\chi^2 = 1.31$, p = 0.425	$\chi^2 = 3.07$, p = 0.179

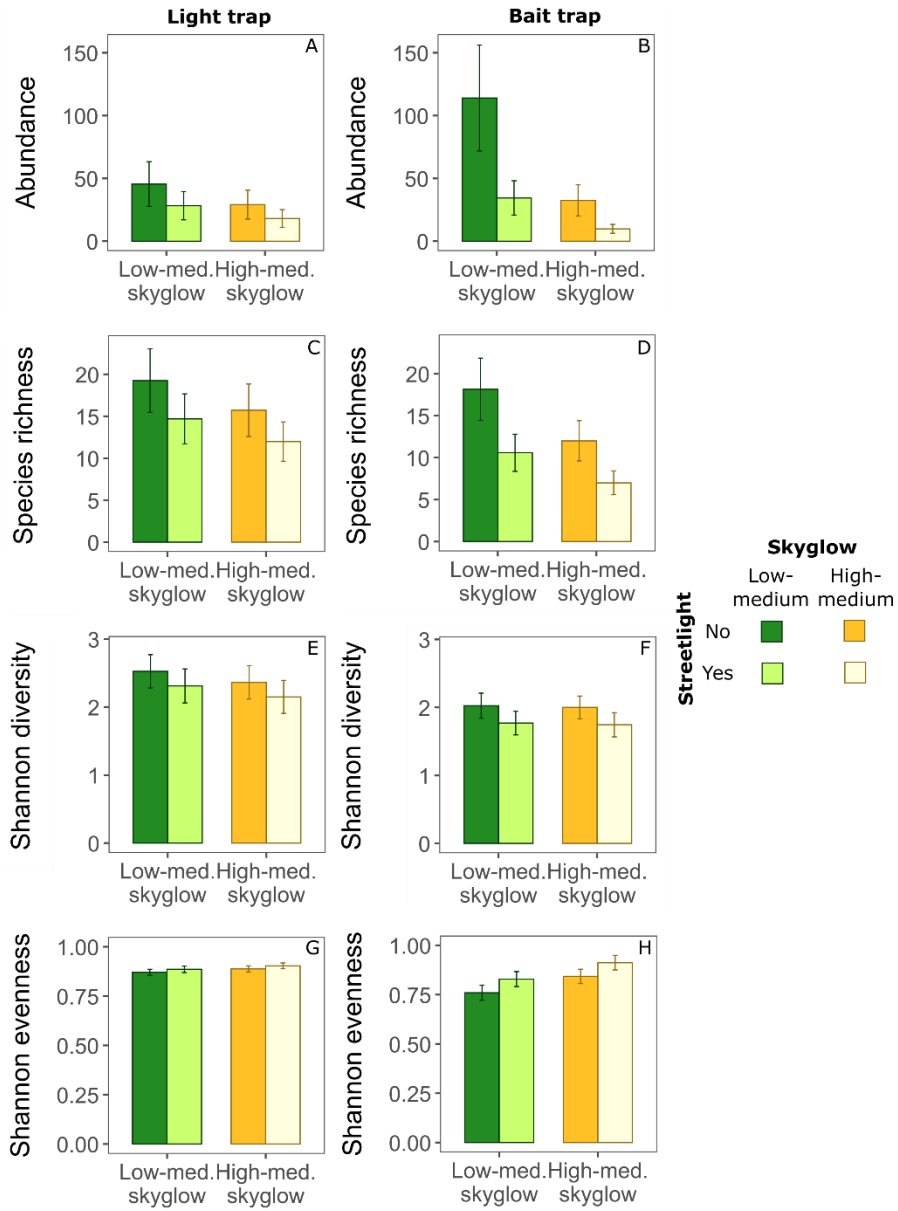


Fig. S6.5. Model parameter estimates $\pm$ SE of moth abundance, species richness, Shannon diversity and Shannon evenness under the sampled skyglow and streetlight conditions for (A,C,E,G) light traps and (B,D,F,H) bait traps; with 4 sampling sites removed.

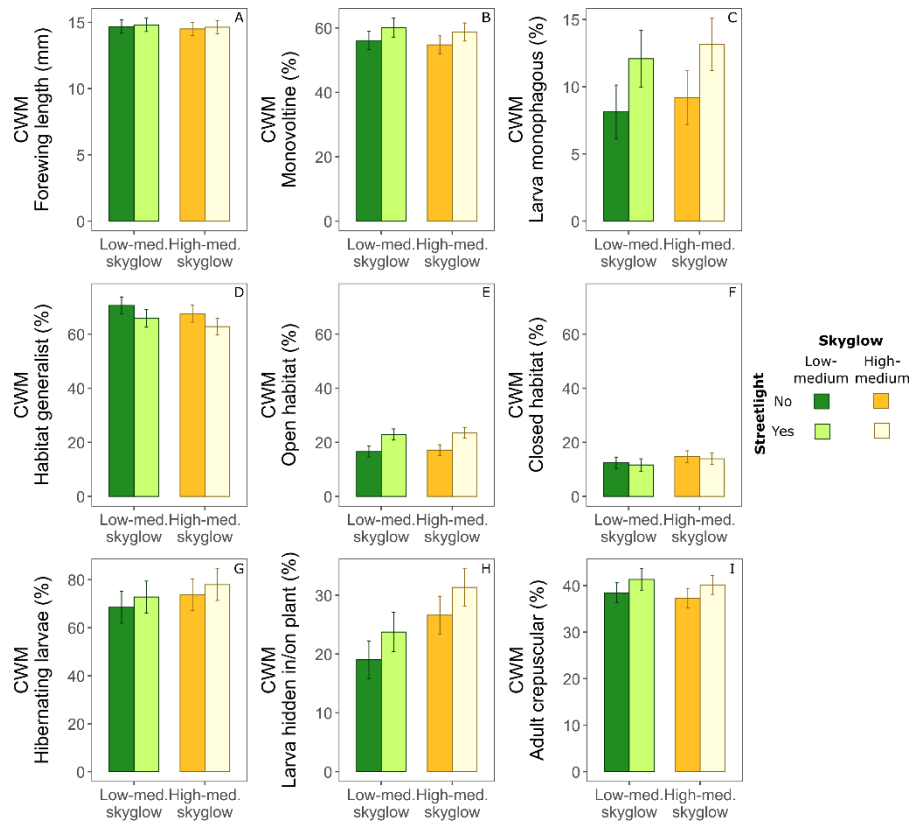


Fig. S6.6. Model parameter estimates $\pm$ SE for community-weighted means of the tested morphological, behavioural and life-history traits under the sampled skyglow and streetlight conditions; with 4 sampling sites removed. Only moths captured with light traps were included.

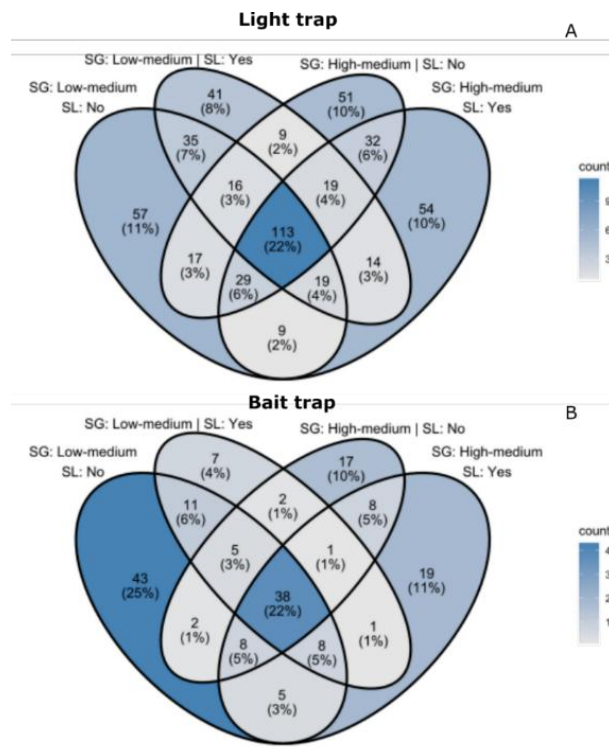


Fig. S6.7. Venn diagrams showing the number (and percentage) of shared species between the different light conditions for (A) light traps and (B) bait traps; with 4 sampling sites removed. SG = skyglow level; SL = streetlight presence.

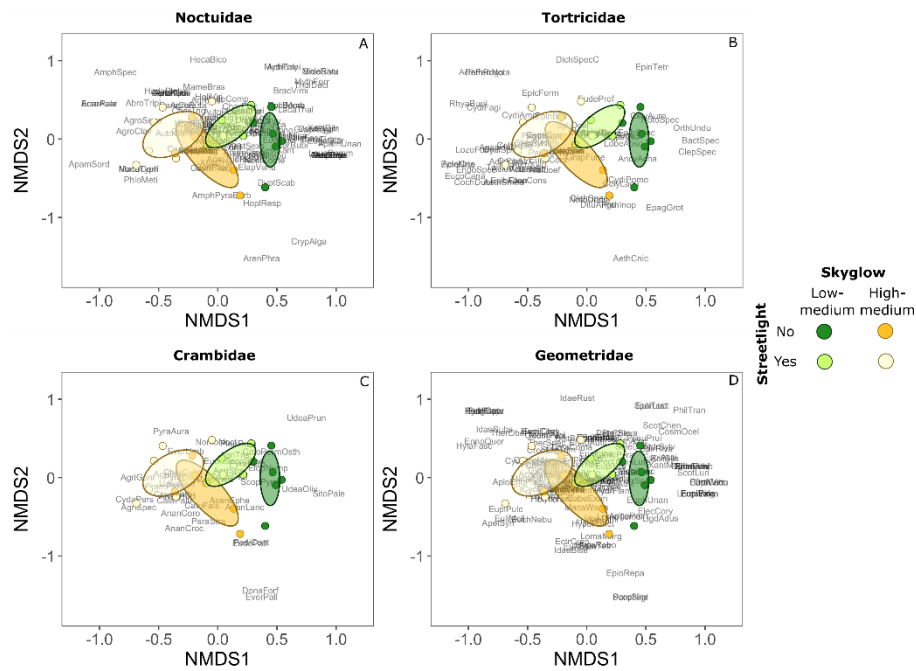


Fig. S6.8. Plot showing non-metric multidimensional scaling with Chord distance based on species abundance in light traps; with 4 sampling sites removed. Dots depict the sampling sites and ellipses show 95 % confidence intervals. Species scores are shown for (A) Noctuidae, (B) Tortricidae, (C) Crambidae and (D) Geometridae. Abbreviations of species names can be found in the dataset.

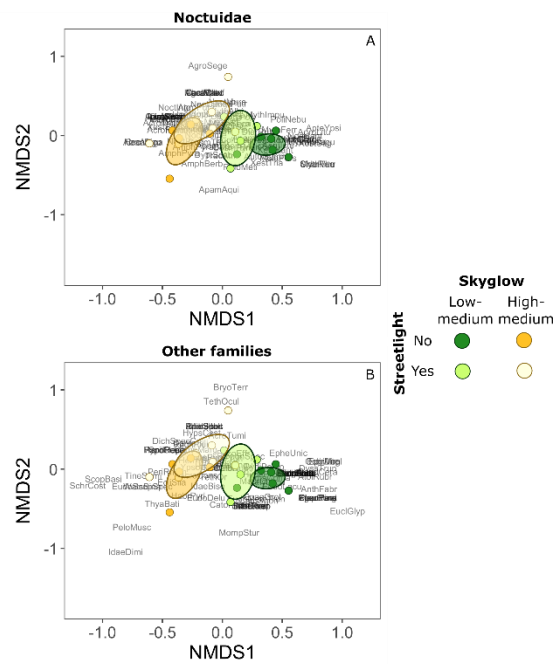


Fig. S6.9. Plot showing non-metric multidimensional scaling with Chord distance based on species abundance in bait traps; with 4 sampling sites removed. Dots depict the sampling sites and ellipses show 95 % confidence intervals. Species scores are shown for (A) Noctuidae and (B) the other moth families. Abbreviations of species names can be found in the dataset.

CHAPTER 7

General Discussion

7.1 Thesis summary and outline of the General discussion

Moths are an emblematic species group in ALAN research due to their flight-to-light response. However, not only their adult behaviour can be directly affected, but also larval development and adult phenotype production can be impacted by ALAN. However, important knowledge gaps still exist, and particularly the consequences for the adult stage have not yet been tested. Despite growing evidence for effects of ALAN in moths, the impact on moth communities had hardly been studied before this PhD thesis (see review in *Chapter 1*). In order to get a deeper view into the impact of light pollution in moths, it is important to get a better understanding of how species with different ecological profiles are affected. In this PhD thesis, we investigated the impact of ALAN on larval development and consequences for adult flight-related morphology as well as the effects of skyglow and direct ALAN on moth communities.

My first aim was to broaden our knowledge on the impact of ALAN on larval development in split-brood rearing experiments. In *Chapter 2*, a capital breeding moth with diurnal caterpillars, which is an understudied ecological profile in this context, showed higher larval mortality, diapause inhibition resulting in faster development and a decrease in female pupal mass when reared under ALAN conditions. Next, we showed evidence for similar, or even stronger effects, of dynamic ALAN on larval development compared to continuous ALAN (*Chapter 3*). Two noctuid moth species from populations with different skyglow levels showed faster development, increased growth rate and higher body mass under ALAN.

Before addressing the question whether larval development under ALAN leads to changes in flight-related morphology (*Chapter 5*), we investigated whether flight-related morphology is related to the flight-to-light response (*Chapter 4*). Moths from urban, light-polluted areas had smaller wings than conspecifics from rural, dark areas. Moreover, wing size was positively related to the flight-to-light response observed by Altermatt and Ebert (2016). In *Chapter 5*, we showed evidence for sex-specific effects of development under ALAN on flight-related morphology, resulting in altered sexual dimorphism. Furthermore, moths reared under ALAN allocated relatively more of their body mass to the abdomen.

Finally, in *Chapter 6*, we set up a full-factorial study design of skyglow and direct streetlight pollution in order to investigate the impact of both types of

light pollution on moth communities. Both skyglow and streetlight pollution significantly reduced moth abundance, and the presence of streetlights also resulted in lower species richness and diversity. Moth composition changed under higher skyglow and near streetlights. Alterations in the relative incidence of moth species traits in these moth communities were related to both skyglow and especially streetlight pollution.

Hence, this PhD thesis provides evidence for ALAN effects on larval development and adult moth morphology. Furthermore, both direct light pollution by streetlights and indirect light pollution by skyglow resulted in altered moth communities. In this General discussion chapter, we will first discuss the potential impact of these results for moth behaviour and life histories as well as the consequences for interactions with other organisms in light-polluted ecosystems. Next, we will discuss whether ecological traits can predict the response of a species to larval development under ALAN, and whether this is reflected in moth communities. Then, anthropogenic changes that typically co-occur with light pollution and can act as confounding factors are discussed. we will also make recommendations for the planning of public lighting. Some critical notes will be put on the interpretation of some of the results and on methodological choices made in different chapters. And finally, we will reflect on pressing questions regarding the impact of ALAN on biodiversity that follow from both the results presented in this PhD thesis and previous research.

7.2 Moths in light-polluted ecosystems

7.2.1 The role of flight and fecundity-related morphology under ALAN

Previous studies have shown a negative impact of larval development under ALAN on body mass (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023), and this was also the case for *Arctia caja* (Van de Schoot *et al.*, 2025c: *Chapter 2*). However, in *Chapter 3* (Van de Schoot *et al.*, 2025a), evidence is shown that the opposite can also occur. Increased and reduced body mass are assumed to result in higher or lower fecundity, respectively, especially in females (Lamunyon, 1997; Heisswolf *et al.*, 2009) and increase or decrease in flight performance (Berwaerts *et al.*, 2002). However, the question is whether this is not too simplistic, as there often is a trade-off between flight capacity and fecundity in flying insects (Tigreros & Davidowitz, 2019). For example, a moth that has a higher body mass can have allocated most of this gained mass to the abdomen with a lower relative increase in thorax mass and wing size, which would cause the thoracic muscles and wings to have to lift a relatively higher mass. In this regard, the results in

Chapter 5 show a significant increase in relative abdomen mass and a relative decrease in thorax mass. This suggests a higher investment in fecundity, assuming that the relationship between abdomen mass and female potential fecundity holds under ALAN conditions, as the number of eggs per given mass can change under different environmental conditions (e.g., Heisswolf *et al.*, 2009; Walczak *et al.*, 2017). Moreover, there can be a trade-off between egg numbers and egg size (e.g., Steigenga & Fischer, 2007). An increased fecundity would evidently be positive for a moth, but the strong reduction in relative thorax mass could constrain flight performance. In females, this reduction can be partially compensated by the increase of mass-corrected wing area, but males had relatively smaller wings under ALAN (*Chapter 5*). If these morphological changes lead to a significant decrease of dispersal capacity, this could have negative consequences for gene flow. However, lower investment in flight-related morphology is not necessarily entirely negative for both daily foraging and dispersal. In *Chapter 4* (Van de Schoot *et al.*, 2024), we showed evidence for a positive relationship between flight-related morphology and flight-to-light behaviour. This suggests a weaker flight-to-light response in *A. exclamatoris* reared under ALAN conditions, which could reduce the negative impact of ALAN on mating behaviour (van Geffen *et al.*, 2015b, 2015a; Storms *et al.*, 2025), adult feeding behaviour (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022) and predation risks (Wakefield *et al.*, 2015; Hermans *et al.*, 2024). In *Chapter 4* (Van de Schoot *et al.*, 2024), however, it was mainly wing size that showed a relationship with flight-to-light behaviour. Future studies will thus have to clarify whether relative thorax mass can also be related to flight-to-light response. Here, it may also be valuable to set up a study with artificial selection both for and against flight-to-light behaviour as well as a control, with at least one replicate each time (Conner, 2003; Laukkanen *et al.*, 2018). Furthermore, it would be interesting to investigate changes in flight- and fecundity-related morphology for species that show reduced body mass after development under ALAN, which we plan to do for the *Arctia caja* specimens from *Chapter 2* (Van de Schoot *et al.*, 2025c).

If morphological changes indeed result in an altered flight-to-light response, and this in turn would have a positive impact on fitness, light pollution could act as a filter for flight-related morphology (as shown for temperature: Chia *et al.*, 2023). At the community level, we did not find evidence for filtering of body size, proxied by mean wing size, by skyglow and streetlight pollution (Van de Schoot *et al.*, 2025b: *Chapter 6*). However, morphological traits are in fact continuous, while here, a single value per species was used. Therefore, it would be interesting to also investigate intraspecific shifts in morphology (*cf.* Merckx *et al.*, 2018), which has not been done yet for our study.

7.2.2 Plant-moth interactions

Moths play an important role as pollinators of both strictly and facultatively night-pollinated plants (*Chapter 1*). Significant reductions in moth abundance related to skyglow and streetlight pollution (Van de Schoot *et al.*, 2025b: *Chapter 6*) can impair this ecosystem service. Moreover, not only pollinator abundance, but also a decline in species richness and diversity, as observed in gardens illuminated by streetlights (Van de Schoot *et al.*, 2025b: *Chapter 6*), can lead to reduced pollinator services if there is a community-level change in flower preference, temporal diversity and/or spatial diversity (Klein, 2009; Genung *et al.*, 2017). Reduced pollinator mobility under light pollution, as suggested by our results in *Chapter 4* (Van de Schoot *et al.*, 2024) and 5, can have negative consequences for gene flow in plants (Öckinger *et al.*, 2018; Feigs *et al.*, 2022). Moreover, ALAN can potentially lead to phenological shifts in moths (Van de Schoot *et al.*, 2025c: *Chapter 2*; Van de Schoot *et al.*, 2025a: *Chapter 3*), which could result in mismatches when these shifts do not parallel those of plant flowering (Kehrberger & Holzschuh, 2019; Kudo & Cooper, 2019). Additionally, it has already been shown that ALAN lowers adult feeding rate (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022) and alters visual perception of flowers in moths (Briolat *et al.*, 2021; Vissio *et al.*, 2024). Taken together, ALAN can be expected to have a negative impact on nocturnal pollination. But the question is whether this is always the case, since existing literature shows variable results. The most studied plant in this regard is *Silene latifolia*, which has a nursery pollination relationship with *Hadena* sp. ALAN effects on the pollination of this plant go from negative (Giavi *et al.*, 2020) to neutral (Boom *et al.*, 2020) in lab experiments where only *Hadena* sp. can visit the plants, but positive effects were found in an open outdoor study system (Macgregor *et al.*, 2019). Other studies found a more consistent negative impact on nocturnal pollination (Knop *et al.*, 2017; Soteras *et al.*, 2022). Diurnal plant-pollinator interactions can also be affected by ALAN. For example, Giavi *et al.* (2021) found variable results on flower visitation depending on plant species and pollinator group. In a specialised nursery pollination relationship between the yucca plant *Hesperoyucca whipplei* and the moth *Tegeticula maculata*, ALAN led to an increase of fruit set (Wilson *et al.*, 2021). It is clear that light pollution can have an impact on pollination, but some important knowledge gaps still remain. For example, given that Wilson *et al.* (2021) showed that skyglow can also affect pollination in a diurnal system, it is now required to study the impact of both skyglow and direct light pollution in nocturnal pollination systems. Further, genetic studies (*cf.* Feigs *et al.*, 2022) still have to clarify

how ALAN affects gene flow in plants pollinated by moths, and by insects in general.

Moths play an important role as herbivores, but light pollution has the potential to alter the timing and intensity of this ecological interaction (Boyes *et al.*, 2021b). For example, many moths that feed on woody plants as a larva have matched their phenology with the presence of young nutritious leaves. However, ALAN can lead to a phenological shift in both moths (Van de Schoot *et al.*, 2025c: *Chapter 2*; Van de Schoot *et al.*, 2025a: *Chapter 3*) and plant bud burst (French-Constant *et al.*, 2016; Meng *et al.*, 2022), which could result in a mismatch. Moreover, plants growing under ALAN conditions have tougher leaves (Grenis & Murphy, 2019; Murphy *et al.*, 2022), which has been shown to significantly reduce herbivory by insects (Cao *et al.*, 2024). Further, studies in plant-moth nursery pollination systems have shown that not only pollination can be affected by ALAN in these systems, but also fruit infestation by the pollinators' larvae can change. In *S. latifolia*, one study showed evidence for increased seed infestation under direct ALAN (Boom *et al.*, 2020). However, another study in the same system showed that seed infestation was higher in dark sites, but only in those adjacent to sites with direct light pollution (Giavi *et al.*, 2020). In the yucca-moth system, fruit infestation only increased with skyglow, but did not change under direct ALAN (Wilson *et al.*, 2021).

When ALAN results in an increased body mass in moths as observed in *Chapter 3* (Van de Schoot *et al.*, 2025a), this likely comes with higher larval herbivory, and this can have consequences for plant flowering. First, herbivory can delay flowering (Brody, 1997; Lemoine *et al.*, 2017), which could lead to a phenological mismatch with the plants' pollinators. In some cases, this could be compensated by a direct promotion of flowering phenology by ALAN (Bennie *et al.*, 2018; Wang *et al.*, 2022), but the opposite can also be the case (Bennie *et al.*, 2018; Lian *et al.*, 2021). Second, increased herbivory can be expected to result in a lower number of flowers, especially when seeds or flowers are eaten (e.g., Pettersson, 1991). This would lead to reduced food availability for adult pollinators. In specialised nursery pollination systems, this would probably result in a negative feedback system, which is often already present to buffer population fluctuations due to changes in environmental conditions. Lower flower availability is likely to result in lower herbivory in the next generation, which in turn would lead to higher flower numbers, and potentially again in higher herbivory (Pettersson, 1991).

7.2.3 Predator-prey interactions

In all their life stages, moths serve as important prey or hosts for other organisms, but especially the egg, larval and adult stages are sought after by different kinds of parasitoids and both invertebrate and vertebrate predators (*Chapter 1*). Previous studies have shown that moths and other insects have a higher risk of predation due to the loss of evasive manoeuvres (Wakefield *et al.*, 2015), the concentration of prey and predators near artificial light sources (Willmott *et al.*, 2019; Hermans *et al.*, 2024), extended predator activity (Evens *et al.*, 2023; Hermans *et al.*, 2024) and higher visibility (Creemers *et al.*, 2025). But the impact ALAN has on moths can also indirectly affect predators. Significant reductions in moth abundance under light pollution (Van de Schoot *et al.*, 2025b: *Chapter 6*) will likely result in lower food availability for many of these organisms, at least locally. Intraspecific shifts towards higher body mass could partially compensate for this loss, but most studies have shown body mass reduction under ALAN (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*; but see Van de Schoot *et al.*, 2025a: *Chapter 3*). However, the impact of ALAN on larvae of important prey species for birds (e.g., *Operophtera brumata* and *Tortrix viridana*) has not yet been studied. Also here, a phenological mismatch between the presence of these larvae and bird nesting can have a detrimental impact for bird fitness (*cf.* phenological shifts due to global warming: e.g., Visser *et al.*, 1998). For bats, a lower availability of moth prey could be compensated by an increase of other prey organisms, including diurnal species, as many bats have quite a varied diet. However, for many of these invertebrates, our knowledge of how they are affected by light pollution is still very limited, and thus urgently requires more scientific attention.

Many moth species and other nocturnal insects have a body colour to match their environment with the aim of being as inconspicuous as possible to predators during the day. Despite the fact that ALAN changes the light intensity and spectrum of the nocturnal environment, and could thus disrupt reliable cues for background matching (Briolat *et al.*, 2021; Bullough *et al.*, 2023), the role of wing colouration in light of ALAN has not yet been investigated. In *Chapter 5*, we give a first indication that wing melanisation can differ between populations originating from regions with different skyglow levels. However, whether such changes have significant implications for a moth in a light-polluted world is not clear. For future research, it is first of all important to gain a better understanding of what cues moths and other insects use to choose a resting spot and whether this depends on their wing colouration. In this regard, it would be interesting to investigate whether the sexes of species with sexual colour dimorphism (e.g., *Agrotis* sp., *Lithosia* sp.,

Archips sp.) select different backgrounds, and whether this leads to sex-specific responses to ALAN. Besides cryptic colouration, also aposematic colouration can be relevant within the topic of light pollution. For example, one of our study species, *Arctia caja*, has orange-red hindwings with black-blue markings to scare-off predators. Studies in a related moth species, *Parasemia plantaginis*, have shown that individuals with more intensely red hindwings are less often attacked by birds, compared to individuals with more orange hindwings (Lindstedt *et al.*, 2011). However, stressful conditions during larval development can result in lighter hindwings as the production of the red pigment is costly (Lindstedt *et al.*, 2010). Since our results in *Chapter 2* (Van de Schoot *et al.*, 2025c) indicate that ALAN exposure during larval development has a negative impact on *Arctia caja*, at least in females, it could be expected that ALAN-treated individuals have more orange hindwings, compared to control specimens. We plan to test this hypothesis using the specimens reared in *Chapter 2* (Van de Schoot *et al.*, 2025c). If true, this would suggest that ALAN leads to reduced effectiveness of aposematism in *Arctia caja*. In addition to experimental work, it would also be valuable to include cryptic and aposematic wing colouration as traits in community studies like *Chapter 6* (Van de Schoot *et al.*, 2025b). However, this would require unambiguous quantification of these traits (*cf.* wing pattern variability: Franzén *et al.*, 2019) for which much experimental work will still be needed.

7.3 Larval development under ALAN: are some species' ecological profiles more sensitive than others?

7.3.1 The role of species traits in moth development

Our research has added new ecological profiles to the field of ALAN effects on larval development in moths. Acceleration of larval development under ALAN conditions has been shown in two moth species with nocturnal larvae that feed openly on top of the host plant (van Geffen *et al.*, 2014; Merckx *et al.*, 2023). This has now been confirmed in two species with different larval behaviour: *Agrotis exclamationis* has larvae with a more hidden lifestyle (Van de Schoot *et al.*, 2025a: *Chapter 3*), and the larvae of *Arctia caja* show a diurnal activity peak (Van de Schoot *et al.*, 2025c: *Chapter 2*). Spending less time in the larval stage is not necessarily negative for a moth, because it, for example, reduces the time to get infected by parasitoids or to be consumed by larvae-eating predators. However, if the changes are too strong, the consequences probably become negative. For species that hibernate as pupae, the observed acceleration is independent of the occurrence of

diapause, and therefore only causes a shift of a few days (van Geffen *et al.*, 2014; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025a: *Chapter 3*). Such small differences are unlikely to cause phenological mismatches with host plants. For species like *Arctia caja* that show larval diapause, duration of larval development is mainly determined by the occurrence of feeding arrest. This consequently results in much stronger shifts, and thus likely in a mismatch with host plant phenology. Moreover, if the inhibition of larval and pupal diapause observed under ALAN (van Geffen *et al.*, 2014; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*) persists in outdoor conditions, this would have a detrimental impact on survival during winter.

Light pollution disturbs the natural day-night cycle and hence changes the activity patterns of different organisms (Le Tallec *et al.*, 2013; Duarte *et al.*, 2019; Wolkoff *et al.*, 2023; Gomes *et al.*, 2024; Grunst *et al.*, 2024; Hermans *et al.*, 2024). Examples in adult insects show that this can lead to reduced feeding activity in nocturnal species (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022), but to an extension of the feeding period into the night for diurnal species (Gomes *et al.*, 2024). If this also applies for the larval stages, we can expect nocturnal larvae to end up with a lower body mass when growing up under ALAN conditions, and *vice versa* for diurnal larvae. Indeed, previous studies in nocturnal larvae were in line with this theory (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023). Interestingly, in contrast to the predictions, the diurnal larvae of *Arctia caja* showed a similar negative impact of ALAN on body mass, albeit only in females (Van de Schoot *et al.*, 2025c: *Chapter 2*). This shows that species with opposite activity patterns can experience a similar impact from ALAN, and broadens the evidence for negative effects of ALAN on larval development in moths. However, unlike the species used in previous studies, *Arctia caja* is a capital breeding species, which means this species has no means to compensate for a lower amount of accumulated resources during the larval stage.

It would be too simplistic to say that larval development is negatively affected by ALAN in all moth species. Both *Agrotis exclamationis* and, less pronounced, *Ochropleura plecta* showed increased body mass, which suggests that larval development is rather positively affected by ALAN in these species (Van de Schoot *et al.*, 2025a: *Chapter 3*). One potential mechanism is an increase of feeding behaviour under ALAN conditions as shown in the butterfly *Danaus plexippus* (Haynes *et al.*, 2023), but no evidence was found for this hypothesis. Interestingly, both species have a similar profile as the species from previous studies, being income breeders with nocturnal larvae. This raises the question whether *Agrotis exclamationis* and *Ochropleura plecta* possess other traits that may explain the positive effects on body mass observed in these species, and whether this is reflected in the relationships we have shown in *Chapter 6* (Van de Schoot *et al.*, 2025b).

Both species have very similar ecological profiles compared to previously studied species, at least for the traits tested in *Chapter 6* (Van de Schoot *et al.*, 2025b). Species that hibernate as larvae showed higher incidence under light pollution, especially compared to pupal hibernators. But the effect of ALAN on larval development varies within both trait values; *Ochropleura plecta* (Van de Schoot *et al.*, 2025a: *Chapter 3*) is a pupal hibernator like *Mamestra brassicae* (van Geffen *et al.*, 2014) and *Chiasmia clathrata* (Merckx *et al.*, 2023), and *Agrotis exclamationis* (Van de Schoot *et al.*, 2025a: *Chapter 3*) is a larval hibernator like *Apamea sordens* (Grenis & Murphy, 2019) and *Arctia caja* (Van de Schoot *et al.*, 2025c: *Chapter 2*). However, if we look more carefully at the larval hibernators, we see that the hibernating larvae of *Agrotis exclamationis* are full-grown and spend winter already in the underground cocoon where they will pupate in spring, while the other two species hibernate in an early larval stage and have to resume feeding in spring. This could make *Agrotis exclamationis* less sensitive to ALAN disturbances related to diapause. However, it should be noted that in our study, hibernation was completely absent in all treatments due to a long photoperiod, and therefore, the impact of ALAN on diapause was not tested in this case (Van de Schoot *et al.*, 2025a: *Chapter 3*).

7.3.2 Are development-related traits filtered at the community level?

In *Chapter 6* (Van de Schoot *et al.*, 2025b), moth communities under light pollution had a higher incidence of species with larvae hidden within their food plant or in a leaf roll. None of the tested species has such a larval habitation. However, despite being categorised as feeding openly on the food plant, larvae of *Agrotis exclamationis* live much more hidden compared to other species with the same trait value. Larvae of this species hide on the soil surface or underground during the day (Waring *et al.*, 2015) and also mainly feed from under the host plant's leaves (own observation). This could reduce exposure to ALAN (Summers *et al.*, 2024), but it does not explain why body mass increased instead of decreased. Potentially, behavioural or physiological changes play an important role here. For future research, it could therefore be interesting to track larval behaviour or to investigate whether energy efficiency changes under ALAN. For now, it thus remains unclear why *Agrotis exclamationis* and *Ochropleura plecta* showed a different response to ALAN during larval development compared to other species. However, the fact is that both species are overall much more abundant, even in a strongly urbanised region as Flanders (www.waarnemingen.be; Van de Schoot *et al.*, 2025b: *Chapter 6*). However, the abundance and presence of *Ochropleura plecta* is clearly negatively

affected by both skyglow and streetlight pollution (Table 7.1). On the other hand, light trap data suggest that *Agrotis exclamatoris* is not affected by light pollution. However, bait trap data indicate a lower abundance in the presence of streetlight, but no clear reduction in incidence. Previous studies have shown an inhibition of adult feeding under ALAN, which may explain this observation (van Langevelde *et al.*, 2017; Cieraad *et al.*, 2022). But this raises the important question whether the efficiency of bait traps is indeed unaffected by ALAN, as is usually assumed (Yela & Holyoak, 1997; Grenis *et al.*, 2023).

Table 7.1. Abundance (and presence) for the species used as study organisms in research on the impact of ALAN on larval development, as observed in Chapter 6.

	Light trap				Bait trap			
	Low-medium skyglow		High-medium skyglow		Low-medium skyglow		High-medium skyglow	
	Dark	Streetl.	Dark	Streetl.	Dark	Streetl.	Dark	Streetl.
<i>A. exclamatoris</i>	57 (19)	54 (21)	57 (16)	78 (23)	33 (8)	19 (7)	23 (8)	8 (7)
<i>A. sordens</i>	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>A. caja</i>	0 (0)	1 (1)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
<i>C. clathrata</i>	0 (0)	2 (2)	2 (2)	9 (7)	0 (0)	0 (0)	0 (0)	0 (0)
<i>M. brassicae</i>	1 (1)	0 (0)	11 (4)	5 (2)	4 (3)	1 (1)	34 (9)	6 (5)
<i>O. plecta</i>	65 (24)	13 (9)	35 (11)	11 (8)	53 (8)	4 (2)	11 (5)	8 (4)

7.3.3 Understudied development-related traits

Although this PhD thesis has managed to fill some important knowledge gaps regarding larval development under ALAN, certain species traits linked to larval development remain unstudied. First, some moth species that hibernate as an egg like *Tortrix viridana* and *Operophtera brumata* are an important food source for birds (Coomes *et al.*, 2024). However, this relationship in population dynamics only seems to be present in simple food webs, while it disappears in more complex systems (Yazdanian *et al.*, 2024). The latter species has already been used to study the effect of ALAN on mating behaviour (van Geffen *et al.*, 2015b), but as mentioned in subsection

7.2.3, the impact on its life cycle is currently unknown. Actually, the impact of ALAN on invertebrate eggs has rarely been studied (Baz *et al.*, 2022), and to the best of my knowledge, has not yet been studied in insects. Also species that hibernate in the adult stage, like the very common *Conistra vaccinii* and *Eupsilia transversa*, have not yet been studied in this regard. Further, it would be interesting to investigate whether ALAN changes the ratio of larval and pupal hibernating individuals in species that exhibit both overwintering strategies like *Phlogophora meticulosa*, but also the butterfly *Pararge aegeria* (Wiklund & Friberg, 2011).

Second, the impact of ALAN on larvae that show strongly hidden feeding behaviour has only rarely been studied. A single study investigated ALAN effects on the development of a leaf-mining micro-moth (Schroer *et al.*, 2019), but despite evidence that plant tissue can reduce the amount of light a larvae experiences (Summers *et al.*, 2024), stem or leaf-roll inhabiting species have not yet been tested. These traits are more present in micro-moths, which are in general an understudied group when it comes to light pollution (Van de Schoot *et al.*, 2025b: Chapter 6).

Third, since species with monophagous larvae cannot switch to another host plant when the latter becomes less suitable under ALAN, it would be interesting to rear monophagous species in a design similar to the study of Grenis and Murphy (2019). They used a full-factorial design of larvae reared under ALAN or dark nights on plants that were either collected at fields illuminated by streetlights or dark fields (Grenis & Murphy, 2019). Furthermore, species feeding on woody plants, mosses or lichens have also largely been ignored (only *Cameraria ohridella*: Schroer *et al.*, 2019).

Fourth, the duration of larval development potentially plays an important role on the strength of the ALAN impact. For example, *Arctia caja* has by far the longest development time of all tested species and it was the only to show increased mortality under ALAN conditions (Van de Schoot *et al.*, 2025c: Chapter 2). However, it should be noted that this trait is strongly correlated to body size and to whether a species hibernates in the larval stage or not. Moreover, multivoltine species can have different development times depending on the generation, and it would therefore be interesting to investigate whether larval responses to ALAN differ between generations.

Other traits worth looking at are the height at which adult moths fly and their larvae live. Several studies that mainly took place in forests have shown that moth communities show vertical stratification, with family-dependent flying heights (e.g., Brehm, 2007; Ashton *et al.*, 2016; De Smedt *et al.*, 2019). Species that fly higher have a lower chance of being attracted to an artificial light source like a streetlight (Degen *et al.*, 2024). Furthermore, larvae living higher than the height of streetlight will receive less direct ALAN than larvae living below a streetlight. This height can also vary between different stages

within a species. For example, some species feeding on low herbs and grasses as a larva, mainly fly at canopy height (i.e., around 30 m: De Smedt *et al.*, 2019). Therefore, larvae and adults of these species may suffer from ALAN to varying degrees. However, before these traits can be used in community studies, we will need better knowledge of the vertical stratification for most species.

Finally, it would be interesting to compare species that have different combinations of traits, also of traits that have already been addressed in existing studies. To achieve this, it could be important to look at other moth families, since only four families have been used so far with four species of Noctuidae (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Van de Schoot *et al.*, 2025a: *Chapter 3*) and one species of Geometridae (Merckx *et al.*, 2023), Erebidae (Van de Schoot *et al.*, 2025c: *Chapter 2*) and Gracillariidae (Schroer *et al.*, 2019). Especially, micro-moths harbour a great variety of the untested traits and trait combinations (Sterling *et al.*, 2012). However, for many micro-moths, certain aspects of their ecology are still unclear. That is one of the reasons that certain life-history traits were not addressed in *Chapter 6* (Van de Schoot *et al.*, 2025b). For example, for many micromoths, there is no literature on whether they feed as adults or not, which is related to income or capital breeding, respectively. The larval activity peak is also unknown for many moth species, both macro- and micro-moths. Another trait, voltinism, was already addressed in *Chapter 6* (Van de Schoot *et al.*, 2025b), but may need further attention in future research; in fact, it was unexpected that monovoltine species showed a higher relative incidence in illuminated gardens. Species that are considered to be monovoltine in Belgium may have multiple generations a year at lower latitudes (Teder, 2020). Facultatively monovoltine species may have stronger flexibility to regulate their life cycle under ALAN, which could reduce negative effects. However, if this results in individuals entering winter at the wrong stage, this would have dire consequences in terms of survival (Van Dyck *et al.*, 2015). Moreover, the time of year in which the adults and larvae of monovoltine species are active potentially determines the amount of time a moth is exposed to ALAN during these stages, and may therefore result in different responses. For example, summer species experience shorter nights as an adult compared to spring or autumn species, and may therefore be less affected by ALAN. However, their larvae potentially experience longer nights if they develop during spring or autumn.

7.4 Confounding factors

This thesis only focussed on the effects of light pollution in moths, and during our experiments and observational community study, we controlled as much as possible for other environmental factors. However, in real-world conditions, multiple environmental factors are typically at play at the same time (Wong & Candolin, 2024). In this section, we will discuss some examples of how light pollution can interact with other anthropogenic stressors.

7.4.1 Man-made environmental changes

Several environmental changes related to urbanisation occur simultaneously with light pollution (Fenoglio *et al.*, 2021; Sanetra *et al.*, 2024). First, a landscape with high levels of habitat fragmentation, like urban environments, usually filters for higher mobility in insects (Slade *et al.*, 2013; Merckx *et al.*, 2018), at least until a certain threshold (Bergerot *et al.*, 2012). However, in *Chapter 4* (Van de Schoot *et al.*, 2024), we provided evidence for a positive relationship between mobility and the propensity of flight-to-light, suggesting that more mobile insects might experience more of the negative effects associated with ALAN. Light pollution does not only interact with habitat fragmentation, but can also strengthen it. Indeed, several studies have shown that ALAN can act as a barrier to dispersal in mammals and moths (Laforge *et al.*, 2019; Degen *et al.*, 2024; Le Tallec *et al.*, 2024); however, responses can vary among species (Degen *et al.*, 2024; Hermans, 2024). Whether habitat fragmentation or light pollution has the strongest filtering effect on mobility is likely to depend on the intrinsic mobility of a species. Second, rising temperatures due to global warming and the urban heat island can affect phenology (Altermatt, 2010; Chick *et al.*, 2019) and body size in insects (Horne *et al.*, 2017; Lövei & Magura, 2022), similarly to light pollution. Studies that simultaneously investigate the impact of temperature and ALAN in insects are still scarce (Tougeron & Sanders, 2023), and with variable results. Miller *et al.* (2017) found synergistic effects of ALAN and higher temperatures on aphid control by ladybirds, while studies on phenology and development mainly found an impact of temperature, and little to no effect of ALAN (Merckx *et al.*, 2021; McNamara *et al.*, 2025). An interaction that has been addressed more often is the one between light and noise pollution. However, by far the majority of studies have focused on birds (Halfwerk & Jerem, 2021), while studies on this topic are rare in insects, but the impact could be underestimated (Classen-Rodríguez *et al.*, 2021). Two studies on cricket development and behaviour have shown variable results with some factors being affected by only one of the two stressors, while the combination of light and noise pollution affected other aspects in an additive or synergistic way (Rebar *et al.*, 2022; Ichikawa & Kuriwada, 2023). Chemical

pollution can act either through toxicity or through disruption of olfactory cues, and both can be expected to interact with light pollution. Since ALAN can disrupt pheromone production (van Geffen *et al.*, 2015a) and male attraction to these pheromones (van Geffen *et al.*, 2015b; Storms *et al.*, 2025), the addition of olfactory pollutants can be expected to result in an even stronger disturbance of mating behaviour. Further, the presence of ALAN could potentially alter sensitivity to toxic chemicals (*cf.* temperature: e.g., Li *et al.*, 2020; Verheyen *et al.*, 2022). This is relevant since La Sorte *et al.* (2023) showed that artificial light sources lure nocturnally migrating birds towards areas with higher amounts of toxins, and it is not unlikely that the same effect occurs in nocturnal insects.

7.4.2 Natural factors

Natural gradients or cycles can act as confounding factors alongside light pollution too. First, variation in the length of day and night increases with latitude. Moths living near or above the polar circle experience very short nights or even nights without darkness during summer. The fact that they are used to live under 'natural light at night' could make them less sensitive to ALAN. Whether such lower sensitivity works through in conspecifics living at lower latitudes or whether there is a gradient of sensitivity to ALAN with latitude is still unclear and needs further investigation (*cf.* Merckx *et al.*, 2023). On the other hand, moths from (sub-)tropical regions experience only low seasonal variation in the natural photoperiod, which could make them more sensitive to light pollution. However, the number of studies on the impact of ALAN in (sub-)tropical as well as in (sub-)polar regions is very scarce.

A second potential natural confounding factor is the moon cycle. The interaction between moonlight intensity and light pollution can go in different directions. For example, in birds, one study showed that the presence of moonlight can overrule the effect of skyglow (Creemers *et al.*, 2025), while another study found that skyglow and streetlights overrule the positive effect of moonlight intensity on bird song. In moths, studies have shown that the moon can be used as a compass during flight, at least in a couple of species (Baker, 1987; Degen *et al.*, 2024; Gao *et al.*, 2024). However, the presence of streetlights can turn this usually straight flight into a more tortuous flight (Degen *et al.*, 2024). Whether skyglow and moonlight have an interactive effect on moth flight behaviour is still unclear, but Warrant *et al.* (2024) showed that skyglow can mask stars that are used as a compass for navigation.

It is gradually becoming clear that light pollution can interact with several other environmental factors. However, at the moment, the number of

studies analysing such additive or interactive effects is still very limited, including in insects. Certain combinations of environmental conditions have not yet been tested at all, such as interactions with skyglow. As the effects of light pollution itself become increasingly clear, there is a growing need to include interactions with other factors in future research.

7.5 Recommendations for the planning of public lighting

Previous studies complemented by the results of this thesis show mainly negative effects of ALAN on biodiversity. Therefore, when scheduling public lighting, we should always ask ourselves the questions: where is it needed, when is it needed, and if it is needed, how can we reduce the impact as much as possible? We will discuss these three questions in the following paragraphs.

Where? – The most straightforward solution would be to remove public lighting where it is not needed. For moths, this would have a locally strong positive impact on their abundance and species richness (Van de Schoot *et al.*, 2025b: *Chapter 6*). However, if streetlights are only removed locally, the impact of skyglow would still remain. Evidence is growing that skyglow not only affects navigation during migration (Torres *et al.*, 2020; Warrant *et al.*, 2024), but also activity (Dyer *et al.*, 2023), development (Merckx *et al.*, 2023) and moth abundances (Grenis *et al.*, 2023; Van de Schoot *et al.*, 2025b: *Chapter 6*). Therefore, it is desirable to also reduce skyglow levels as much as possible, prioritizing areas around protected habitats with higher biodiversity, which usually do not receive direct ALAN, but are still at risk of light pollution due to skyglow (Guetté *et al.*, 2018; Jägerbrand & Bouroussis, 2021). This would require the removal of public lighting at a much larger scale to create dark-sky areas (Sordello *et al.*, 2022). However, due to the trade-off with safety and its perception (Haans & de Kort, 2012; Peña-García *et al.*, 2015), this is often hard to achieve, especially in densely populated regions like Belgium, and Flanders in particular.

When? – In case the use of public lighting cannot be avoided, it is important to reduce its impact as much as possible. To do so, new lighting technologies, that can serve this purpose in several ways, are being implemented at a growing extent. A first way is to limit the presence of ALAN to the time when it is needed. This can be achieved by using lighting systems with either motion detection or pre-set timing of a dark period. These measures have the potential to significantly reduce the attraction of insects (Bolliger *et al.*, 2020). However, most nocturnal insects are active at the moment the lights are effectively on (Hao *et al.*, 2023; Kasai & Hironaka, 2024), thus limiting the positive effect. Moreover, a couple of studies have

shown that this part-night or dynamic ALAN can also have an impact on aphid abundances (Heinen *et al.*, 2023), moth flight behaviour (Fabusova *et al.*, 2024), larval development and morphology (Van de Schoot *et al.*, 2025a: *Chapter 3; Chapter 5*). Its effects are sometimes even stronger than full-night or continuous ALAN (Heinen *et al.*, 2023; Van de Schoot *et al.*, 2025a: *Chapter 3; Chapter 5*). The mechanism behind these results is unclear, but Owens *et al.* (2024) suggested that dynamic ALAN results in an even stronger disruption of the natural day-night cycle (going from daylight to relative darkness under dim lighting and then to natural darkness), compared to continuous ALAN (from daylight to relative darkness). Given the large scale at which this type of lighting technology is currently being deployed, including in Belgium (*Chapter 1*), it will be important to further investigate its effects on biodiversity.

How? – A second way is to avoid the spilling of ALAN into the environment. This can be done by directing and/or shielding the light beam so that it focuses only on the targeted illuminated area (Dietenberger *et al.*, 2024). This can significantly reduce the attraction of insect towards artificial light sources (Bolliger *et al.*, 2022; Dietenberger *et al.*, 2024, but see van Koppenhagen *et al.*, 2024). Moreover, these lights can be expected to contribute less to skyglow, and to have a lower impact on, for example, development as food plants receive less ALAN. In this regard, the presence of trees alongside public lighting can also be a promising feature for mitigation; animals living on the illuminated side of the trees would still be affected by ALAN, but further spilling of ALAN into the environment will be reduced (Straka *et al.*, 2019, 2021). However, it should be noted that the illuminated surface will reflect some light, leaving a small amount of ALAN to still spill into the environment and sky (Kocifaj *et al.*, 2024). At the same time, it is also recommended to reduce the amount of short-wavelength light, because most insects (van Langevelde *et al.*, 2011; Donners *et al.*, 2018; Corsini *et al.*, 2025) and bats (Spoelstra *et al.*, 2017) are more strongly affected by it. Especially, the use of monochromatic orange or red lighting is effective in reducing insect attraction, while there is no strong evidence that warm white light is better compared to cold white light (Owens *et al.*, 2024). Red light can also mitigate the impact on larval development, compared to short-wavelength ALAN (van Geffen *et al.*, 2014). However, van Grunsven *et al.* (2020) showed that after a few years of exposure to ALAN, moth abundances decrease equally strong under white, green and red lighting.

While, for now, there does not seem to be one single perfect solution to completely reduce the impact of light pollution due to trade-offs with safety and safety perception, it is certainly important to try to avoid it as much as possible, especially in protected areas that are already under strong pressure from other stressors.

7.6 Critical notes

7.6.1 Interpretation results Chapter 3

In *Chapter 3* (Van de Schoot *et al.*, 2025a), we showed faster larval development, higher growth rate and increased adult body mass under ALAN conditions. We interpreted these results as positive for the moth as this can reduce the time larvae are exposed to predators and parasitoids, and higher body mass can be positively related with fecundity and flight performance. However, these results may not be positive on the long term. Therefore, more nuance is required here. First, an acceleration of larval development can result in a phenological mismatch with host and nectar plants. Although this was only a difference of a few days in our study, it can begin to accumulate in the longer term if not compensated by longer duration of other stages. Moreover, a shorter development time may encourage a moth to produce an extra generation at the end of the flying season. This can lead to a developmental trap when this extra generation cannot develop to the overwintering stage in time and we can hence speak of a lost generation (as hypothesized for climate warming: Van Dyck *et al.*, 2015). Second, higher body mass does not necessarily result in both increased fecundity and flight performance as there is often a trade-off (Tigreros & Davidowitz, 2019). For example, we showed that individuals grown under ALAN conditions allocated a higher proportion of their body mass to the abdomen and a lower proportion to the thorax (*Chapter 5*). This is likely to result in higher fecundity (Lamunyon, 1997; Heisswolf *et al.*, 2009), which is positive, also in the longer term. However, the lower investment in thorax muscles could reduce flight performance (Berwaerts *et al.*, 2002), which can be negative at both the short term (e.g., reduced predator avoidance: Chai & Srygley, 1990) and long term (e.g., lower dispersal capacity and gene flow).

Hence, care must always be taken when describing an effect as positive for a species. This may be true in the very short term, but in the longer term these effects could potentially turn out to be negative for their fitness.

7.6.2 Potential causes for altered flight-related morphology in Chapter 4

We showed evidence for smaller wings in urban *Yponomeuta cagnagella*, and for a positive relationship between wing size and the flight-to-light response (Van de Schoot *et al.*, 2024: *Chapter 4*). We interpreted this change in flight-related morphology as a potential adaptation to avoid the negative impact of flight-to-light, and also discussed habitat fragmentation as a possible confounding factor. However, there are other factors that can have

resulted in the observed lower size in urban moths, two of which we will now briefly discuss. First, urban areas are usually warmer than rural areas (i.e., urban heat island: *Chapter 1*), and insects are often smaller under warmer conditions (Forster *et al.*, 2012). Therefore, the urban heat island may at least partially explain the observed reductions in wing size in urban populations. Second, urbanisation alters predation risk. For example, predation by birds can increase in urban gardens (Frey *et al.*, 2018). Moreover, ALAN may indirectly increase the risk of predation as, for example, pipistrelle bats use streetlights to hunt the increased concentration of insects (Hermans *et al.*, 2023). The presence of insectivorous predators can result in lower body mass in insect populations as shown for bumblebees in places where bee-eaters occur (Kahnt *et al.*, 2025).

Potentially, multiple factors simultaneously put selective pressure on body size in urban insect populations. This again shows the complexity of disentangling the effects of light pollution from other urbanisation-related environmental changes.

7.6.3 Methodological reflections concerning *Chapter 6*

Despite the fact that the results have already been published, it is valuable to discuss two methodological choices made in *Chapter 6* (Van de Schoot *et al.*, 2025b). First, one of the diversity measures we calculated was moth species richness. We showed that, for both light and bait traps, moth species richness was significantly lower under streetlight pollution and lower, though not significant, under higher skyglow levels. However, we did not take into account that the size of regional species pools may be differing between Central (high-medium skyglow) and Southern Belgium (low-medium skyglow). Our high-medium skyglow region (1854 species) has only 86 % of the number of moth species in our low-medium skyglow region (2134 species) (De Prins & Steeman, 2003). One possibility to correct for this difference is the calculation of a relative moth species richness per light trap night or bait trap sample as the number of species observed divided by the size of the regional species pool (*cf.* Cam *et al.*, 2000), or more simply for our dataset, by multiplying species richness at sites under low-medium skyglow with 1854/2134. When we do this for our dataset in *Chapter 6* (Van de Schoot *et al.*, 2025b) and perform the same analyses, relative species richness is still significantly lower in gardens illuminated by streetlights (light trap: $\chi^2 = 8.43$, $p = 0.011$; bait trap: $\chi^2 = 8.45$, $p = 0.011$; Fig. 7.1). The differences related to skyglow were already not significant in our original analysis, but are now also qualitatively absent (light trap: $\chi^2 = 0.00$, $p = 0.982$) or smaller (bait trap: $\chi^2 = 0.83$, $p = 0.434$). However, this methodology also has its disadvantages. For

example, a good knowledge of the local species pool is needed, which is the case for moths in Belgium, but this is often not the case for other regions and species groups. Furthermore, the relative size of the regional species pools may depend on the trapping method as different species pools can be sampled with light and bait traps (Van de Schoot *et al.*, 2025b: Chapter 6).

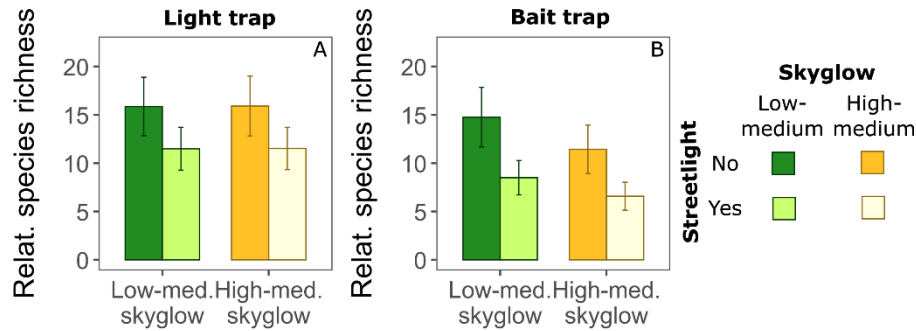


Fig. 7.1. Model parameter estimates $\pm$ SE of relative moth species richness under the sampled skyglow and streetlight conditions for (A) light traps and (B) bait traps.

Second, we calculated trait community-weighted means (CWM) based on presence-absence data, but if abundance data are available, it is more common to weigh CWM for abundance (Zelený, 2018). The reasoning behind our choice not to correct for abundance was that this way the influence of local outbreaks of some species such as *Tortrix viridana*, *Atolmis rubricollis* and *Xestia xanthographa* can be eliminated. However, our choice of statistical model with CWM data for each individual light trap night and the inclusion of day, year and garden location as random variables could already correct for these local outbreaks. When we do the same analyses for abundance-weighted CWM, we can observe that the outcome is mostly qualitatively similar to our original results presented in Chapter 6 (Van de Schoot *et al.*, 2025b) (Fig. 7.2), but significance levels are usually lower, potentially due to the dominance of certain moth species in the communities. However, species abundances are also an important part of community composition. Since analyses with presence-absence CWM and abundance-weighted CWM can give different results, it can be valuable to include both approaches in future trait-based analyses (*cf.* Cingolani *et al.*, 2007).

Table 7.2. Statistical output for differences in trait community weighted means in the light traps (weighted for abundance). The interaction between skyglow and streetlights was non-significant and thus removed from our models. All tests are based on d.f. = 1. P-values were corrected for multiple testing using the Benjamini-Hochberg method. Significant p-values (< 0.05) are given in bold, whereas statistical trend values reflecting weaker evidence (< 0.1) are indicated with a ° symbol.

	Skyglow	Streetlight	Night temperature
Forewing length	$\chi^2 = 0.02, p = 0.923$	$\chi^2 = 3.01, p = 0.203$	$\chi^2 = 7.48, p = 0.056^\circ$
Monovoltine	$\chi^2 = 6.44, p = 0.058^\circ$	$\chi^2 = 6.19, p = 0.058^\circ$	$\chi^2 = 1.27, p = 0.413$
Larva monophagous	$\chi^2 = 2.45, p = 0.265$	$\chi^2 = 4.88, p = 0.082^\circ$	$\chi^2 = 8.05, p = 0.056^\circ$
Habitat generalist	$\chi^2 = 0.93, p = 0.501$	$\chi^2 = 4.50, p = 0.091^\circ$	$\chi^2 = 5.01, p = 0.082$
Open habitats	$\chi^2 = 0.04, p = 0.924$	$\chi^2 = 10.49, p = 0.032$	$\chi^2 = 0.30, p = 0.718$
Closed habitats	$\chi^2 = 2.12, p = 0.300$	$\chi^2 = 0.25, p = 0.722$	$\chi^2 = 6.84, p = 0.058^\circ$
Larval hibernation	$\chi^2 = 0.67, p = 0.589$	$\chi^2 = 2.01, p = 0.300$	$\chi^2 = 0.01, p = 0.925$
Larva hidden in food plant or in rolled-up leaf	$\chi^2 = 5.13, p = 0.082^\circ$	$\chi^2 = 0.30, p = 0.717$	$\chi^2 = 0.46, p = 0.670$
Adult crepuscular	$\chi^2 = 0.02, p = 0.923$	$\chi^2 = 1.72, p = 0.342$	$\chi^2 = 1.44, p = 0.388$

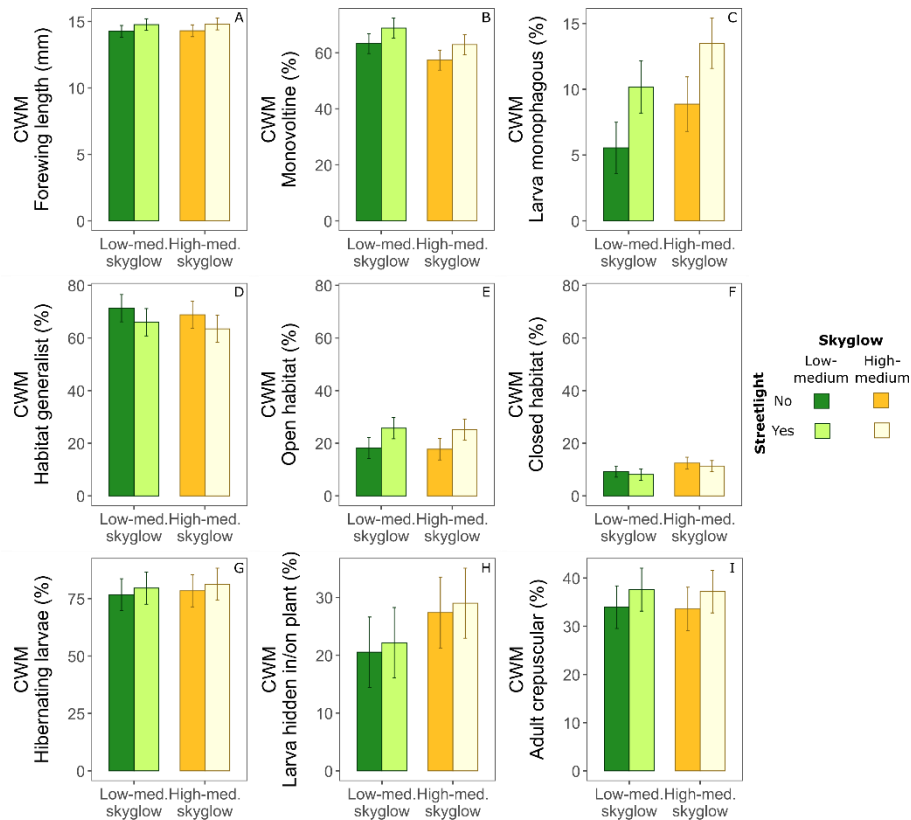


Fig. 7.2. Trait community weighted means based on abundance data – Model parameter estimates $\pm$ SE for community-weighted means (weighted for abundance) of the tested morphological, behavioural and life-history traits under the sampled skyglow and streetlight conditions. Only moths captured with light traps were included.

7.7 Perspectives: where to go from here?

This PhD thesis has extended our knowledge on the impact of ALAN on larval development (Van de Schoot *et al.*, 2025c: *Chapter 2*; Van de Schoot *et al.*, 2025a: *Chapter 3*), showed evidence for sex-specific alterations of body size (Van de Schoot *et al.*, 2025c: *Chapter 2*; *Chapter 5*) and flight-related morphology (*Chapter 5*) and its relationship with flight-to-light behaviour (Van de Schoot *et al.*, 2024: *Chapter 4*). Moreover, we provided evidence for negative effects of skyglow and streetlight pollution on moth communities, and for relationships of both types of light pollution with species trait differences at the community level (Van de Schoot *et al.*, 2025b: *Chapter 6*).

Our results, combined with those of previous studies, open up perspectives for future research. In this section, we will discuss some of those key questions in ALAN research.

Our full-factorial study design applied with dark and illuminated gardens in two regions with different skyglow levels, as applied in *Chapter 6* (Van de Schoot *et al.*, 2025b), allowed for simultaneous testing of the impact of skyglow and streetlight pollution on moth communities. Direct ALAN sources can be expected to have a bigger impact in areas with zero or weak skyglow compared to areas with high skyglow levels, but we found no evidence for an interaction between both types of light pollution. However, it must be noted that in our study region Belgium, skyglow levels are at least low-medium and completely dark skies are not found (Falchi *et al.*, 2016), which may explain the lack of interaction effects. To get a better understanding of the large-scale combined impact of direct light pollution and skyglow, there is a need for studies with a similar study design, but spread over multiple regions with different skyglow levels, including zero and low skyglow. To obtain these different skyglow levels, collaboration between research teams is required.

Such a large-scale full-factorial design can also be used to investigate adaptations related to ALAN. In moths, only one study showed evidence for evolutionary change in flight-to-light behaviour (Altermatt & Ebert, 2016). In *Chapter 3* (Van de Schoot *et al.*, 2025a) and *Chapter 5*, we investigated whether moths originating from a region with higher skyglow levels showed adaptive responses for development under ALAN, but we found no evidence for this hypothesis. Similarly, Cieraad *et al.* (2022) found no evidence for adaptive responses in feeding behaviour and mate calling. However, in both this and our studies, the 'dark' collection sites were never really dark due to skyglow, in contrast to the collection sites used by Altermatt and Ebert (2016). A study design as proposed in the previous paragraph may help resolve the question whether adaptive responses to ALAN are present at a larger scale and in other life-history and behavioural traits.

Evidence is compiling on the impact of ALAN on larval development in insects. The most worrying results are the often-observed body mass reductions (van Geffen *et al.*, 2014; Grenis & Murphy, 2019; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*; but see Durrant *et al.*, 2018; Van de Schoot *et al.*, 2025a: *Chapter 3*) and diapause inhibition (van Geffen *et al.*, 2014; Schroer *et al.*, 2019; Fyie *et al.*, 2021; Merckx *et al.*, 2023; Van de Schoot *et al.*, 2025c: *Chapter 2*). However, all these studies took place in laboratory conditions, with constant temperature, humidity and photoperiod, and sometimes unrealistic ALAN conditions. In the field, environmental conditions vary over time and can, together with the moon cycle, act as confounding factors. Therefore, we argue that the next step is

to perform such experiments outdoors. Reciprocal transplant experiments in which insects originating from dark areas are allowed to develop in small enclosures under realistic ALAN conditions, and *vice versa*, simultaneously allow testing for adaptive responses related to development under ALAN conditions.

We have shown that the impact of ALAN can be species-specific, trait-specific and dependent on the ALAN treatment. However, the mechanisms behind some of our results are still unclear. One example can be found in *Chapter 3* (Van de Schoot *et al.*, 2025a) and *Chapter 5*; in contrast to other studies, *Agrotis exclamationis* showed a positive response of body mass to development under ALAN. Moreover, this effect was sometimes even stronger under dynamic ALAN than under continuous ALAN, but it was also sex-specific. Addressing changes in behaviour (Haynes *et al.*, 2023), physiology (Jones *et al.*, 2015; Durrant *et al.*, 2020a) and gene expression (Orsucci *et al.*, 2018) in such developmental studies can help reveal the mechanism behind these results (Desouhant *et al.*, 2019).

As mentioned in *Chapter 3* (Van de Schoot *et al.*, 2025a), legal frameworks require evidence of negative effects on populations before a unified policy on ALAN regulation can be obtained. However, evidence on whether the lethal and sublethal effects of ALAN on moths and other organisms result in population declines is still lacking. In fact, it is often hard to prove, so we will have to find a way to address this pressing question.

Finally, studies on the impact of ALAN in insects are strongly biased towards a few species groups. If we look at the Lepidoptera, nearly all studies have focused on moths due to their nocturnal activity and flight-to-light response. However, it is not unlikely that butterflies can also be affected by ALAN. For example, larval development could be affected under ALAN, both in species with diurnal larvae (*cf.* Van de Schoot *et al.*, 2025c: *Chapter 2*) as for species with at least partially nocturnal larvae like *Pararge aegeria* (Emmet & Heath, 1989) and *Danaus plexippus* (Haynes *et al.*, 2023). Moreover, flight-to-light behaviour has, to some extent, also recently been reported in butterflies with some individuals ending up under porch lights (Deutsch *et al.*, 2025) or in light traps (www.waarnemingen.be and personal observations). Further, as discussed in *subsection 7.4.2*, sensitivity to ALAN may decrease with latitude (Desouhant *et al.*, 2019). Thus, to obtain a global understanding of the impact of ALAN on biodiversity, it will be important to extend the research field to other species groups (e.g., other pollinating insects, detritivorous invertebrates, aphids, etc.) across all geographical regions.

I would argue that my PhD work made a significant contribution to the field, but much more work is needed to grasp the full ecological and evolutionary impact of ALAN for moths and several other species and how

we can translate this knowledge and insight into efficient evidence-based conservation policy within and outside nature reserves. A challenge of great format.

Index Lepidoptera species



Ch 1 2 3 4 5 6 7
Agriphila sp.
Grasmot onb.
Crambus indet.
Agriphila sp.



Ch 1 2 3 4 5 6 7
Agrotis exclamationis
Gewone worteluil
Point d'exclamation
Heart-and-dart



Ch 1 2 3 4 5 6 7
Apamea sordens
Kweekgrasuil
Noctuelle basilaire
Rustic shoulder-knot



Ch 1 2 3 4 5 6 7
Arctia caja
Grote beer
Ecaïlle martre
Garden tiger moth



Ch 1 2 3 4 5 6 7
Atolmis rubricollis
Zwart beertje
Veuve
Red-necked footman



Ch 1 2 3 4 5 6 7
Bombyx mori
Zijdevlinder
Bombyx du mûrier
Domestic silk moth



Ch 1 2 3 4 5 6 7
Cameraria ohridella
Paardenkastanjemineermot
Teigne du marronnier
Horse chestnut leaf-miner



Ch 1 2 3 4 5 6 7
Celypha lacunana
Brandnetelbladroller
Tordeuse du fraisier
Common marble



Ch 1 2 3 4 5 6 7
Celypha striana
Paardenbloembladroller
Séricore striée
Barred marble



Ch 1 2 3 4 5 6 7
Chiasmia clathrata
Klaverspanner
Géomètre à barreaux
Latticed heath



Ch 1 2 3 4 5 6 7
Chrysoteuchia culmella
Gewone grasmot
Crambus des jardins
Garden grass-veneer



Ch 1 2 3 4 5 6 7
Conistra vaccinii
Bosbesuil
Robuste
Chestnut



Ch 1 2 3 4 5 6 7
Danaus plexippus
Monarchvlinder
Monarque
Monarch butterfly



Ch 1 2 3 4 5 6 7
Diarsia rubi
Gewone breedvleugeluil
Noctuelle belle
Small square-spot



Ch 1 2 3 4 5 6 7
Eupsilia transversa
Wachtervlinder
Satellite
Satellite



Ch 1 2 3 4 5 6 7
Hadena sp.
 Silene-uil onb.
Hadena indet.
Hadena unident..



Ch 1 2 3 4 5 6 7
Mamestra brassicae
 Kooluil
 Brassicaire
 Cabbage moth



Ch 1 2 3 4 5 6 7
Mythimna albipuncta
 Witstipgrasuil
 Point blanc
 White-point



Ch 1 2 3 4 5 6 7
Ochropleura plecta
 Haarbos
 Cordon blanc
 Flame shoulder



Ch 1 2 3 4 5 6 7
Operophtera brumata
 Kleine wintervlinder
 Phalène brumeuse
 Winter moth



Ch 1 2 3 4 5 6 7
Pararge aegeria
 Bont zandoogje
 Tircis
 Speckled wood



Ch 1 2 3 4 5 6 7
Phlogophora meticulosa
 Agaathvlinder
 Craintive
 Angle shades



Ch 1 2 3 4 5 6 7
Platyptilia gonodactyla
 Hoefbladvedermot
 Ptérophore du tussilage
 Triangle plume



Ch 1 2 3 4 5 6 7
Plutella xylostella
 Koolmotje
 Teigne des crucifères
 Diamondback moth



Ch 1 2 3 4 5 6 7
Pyrausta despicata
 Weegbreemot
 Pyrauste du plantain
 Straw-barred pearl



Ch 1 2 3 4 5 6 7
Spilosoma lubricipeda
 Witte tijger
 Ecaille tigrée
 White ermine



Ch 1 2 3 4 5 6 7
Tegeticula maculata
 Yuccamot
Tegeticula maculata
 Yucca moth



Ch 1 2 3 4 5 6 7
Tortrix viridana
 Groene eikenbladroller
 Tordeuse verte du chêne
 Green oak tortrix



Ch 1 2 3 4 5 6 7
Xestia xanthographa
 Vierkantvlekuijl
 Xanthographe
 Square-spot rustic



Ch 1 2 3 4 5 6 7
Yponomeuta cagnagella
 Kardinaalsmutsstippelmot
 Grand hyponomeute du fusain
 Spindle ermine

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