



# Impact of light pollution on moth morphology – A 137-year study in Germany

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## Abstract

Increasing artificial illumination during night has multifaceted effects on species. Moths are shown to be distracted and attracted by artificial light sources, leading to increased mortality through predation or exhaustion. Increased mortality can be expected to increase selection pressure on morphology, particularly those being functional in light detection and flight ability. We were thus interested if intraspecific traits differ between areas and times with differing light pollution values. We chose the moth *Agrotis exclamationis*, a common species in the Berlin-Brandenburg region, Germany, a region that offers very different levels of light pollution across space and time. We examined body length, eye size and forewing length, traits likely targeted through selection due to light pollution. We examined moths collected over the past 137 years. We predicted decreasing forewing length, body and eye size, in response to increasing light pollution and expected to see trait changes from the past to today, and from rural to urban areas, representing temporal and spatial gradients of increasing light pollution. In order to determine current levels of light pollution, we used radiance values of the years 2012 to 2019. These values were the base to extrapolate previous radiance values for all sample sites and years. We observed no trait differences along the spatial gradient, but trait and sex dependant changes along the temporal gradient. We could not confirm a direct causal link between changes in body size and female eye size. However, we revealed indirect effects of light pollution, and assume habitat fragmentation and host-plants to be the main drivers for these effects. A trend towards smaller-eyed females in ‘medium’ and ‘high’ light-polluted areas over time could be a first indication that morphological trait changes to light pollution are taking place.

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**Keywords:** *Agrotis exclamationis*; Radiance; Morphological traits; Body length; Eye size; Wing length; Anthropogenic gradient

## Introduction

Artificial light at night (ALAN) is widespread, positively correlated with urbanisation (Sutton, 2003), and increases at an annual rate of about 2–6% worldwide (Hölker et al.,

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2010a; Kyba et al., 2017b). Because ALAN has been introduced in places, times and at intensities at which it does not naturally occur, it became a threat to biodiversity (Gaston, Visser & Hölker, 2015; Hölker, Wolter, Perkin & Tockner, 2010b; Longcore & Rich, 2004), with respective ecological and evolutionary consequences (Hopkins, Gaston, Visser, Elgar & Jones, 2018; Navara & Nelson, 2007; Rich & Longcore, 2006). Insects, especially moths, seem to be particularly affected by ALAN (Owens et al., 2020; Van Langevelde, Ettema, Donners, WallisDeVries & Groenendijk, 2011). In clear nights moths use celestial light sources such as moon and stars for orientation (e.g. Baker & Sadovy, 1978). However, they get distracted by artificial light and often stay trapped flying around lamps. There they become easy prey to predators or simply die by exhaustion (Degen et al., 2016; Eisenbeis, 2006). Natural selection thus should favour individuals that are less attracted by artificial light sources (Gaston, Bennie, Davies & Hopkins, 2013), as it was shown for populations of ermine moths *Yponomeuta cagnagella*, where specimens from urban areas show a reduced flight-to-light behaviour compared to conspecifics from pristine dark-sky habitats (Altermatt & Ebert, 2016). Morphological trait changes that reduce flight-to-light behaviour may thus indicate adaptation to ALAN in moths. Flight ability is important to meet mates, disperse, escape from predators, and search for nectar and larval host-plants (Chai & Srygley, 1990; Scoble, 1992). Longer-winged specimens have better flight abilities than shorter-winged ones (Beall & Williams, 1945); and larger specimens have been shown to be better dispersers than smaller ones (Nieminen, Rita & Uuvana, 1999; Slade et al., 2013). Specimens with better flight abilities might be relatively more often attracted by ALAN, because they cover larger distances and thus the chances that they come close to artificial light increases (Van Langevelde et al., 2011). Visual cues are important for navigation strategies (Wehner, 1984). Although males' mate detection is primarily based on sex pheromones, visual cues are additively used for short-distance detection (Grant, 1987). In females visual cues are important for selecting host-plants for oviposition (Bernays, 2001). Moth's eye size likewise impacts sensitivity to light (Yack, Johnson, Brown & Warrant, 2007). For instance, Rutowski, Gislén and Warrant (2009) showed that large moths with relatively larger eyes have more accurate and more sensitive vision than smaller individuals, and, species with larger eyes are usually more affected by artificial light than smaller eyed ones (Van Langevelde et al., 2011). Thus, increasing ALAN may select for smaller-eyed individuals.

Because trait change takes place across many generations, it is difficult to observe respective processes within usual study periods. However, this challenge might be overcome by examining museum vouchers, which have been collected over long periods (Doudna & Danielson, 2015; Keinath, Frisch, Müller, Mayer & Rödel, 2020; Nemeier, Müller, Struck & Rödel, 2020). Herein we

investigated the moth *Agrotis exclamationis*. During the last 137 years this species was regularly collected in the German Berlin-Brandenburg area, a region exhibiting steep temporal and spatial gradients of light pollution. We hypothesize a decrease in body size, relative forewing length and eye size due to less mobility and sensitive vision from low to high levels of light pollution, in space and time (Fig. 1).

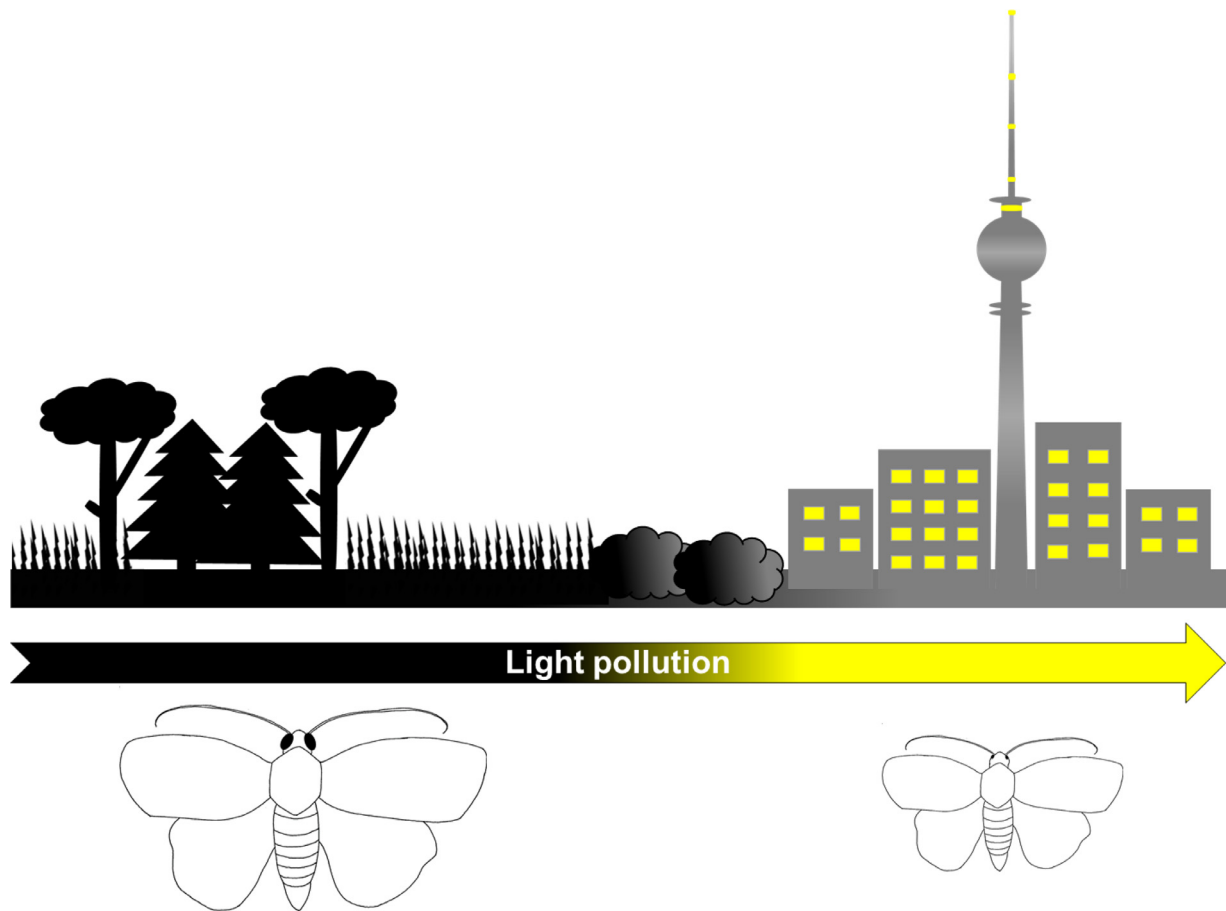
## Materials and methods

### Study area

Berlin, Germany, is an increasingly urbanizing city (Antrop, 2000), including growing levels of light pollution (Kyba et al., 2017b). In contrast, the federal state of Brandenburg, a rural area surrounding Berlin, is mostly consisting of agricultural and near-natural environments (Antrop, 2000; Cochrane & Jonas, 1999). Industrialization in Berlin started in the beginning of the 19th century (Ribbe, Bohm, Schich & Schulz, 2002a). Streets and public places became first artificially illuminated in 1882 (Haubner, 1962). Berlin's population was steadily increasing and reached an unrivalled peak in the 1920s (Ribbe, Bohm, Schich & Schulz, 2002b), comprising a much lower human population after World War II (Ribbe et al., 2002b). Since an economic boom starting in the 1950s onward, the human population and the density and intensity of artificial light increased (Eisenbeis & Hänel, 2009; United Nations, 2002). For instance, Kyba, Kuester and Kuechly (2017a) demonstrated an increase of lit areas of 2.5% and an increase in radiance of 7.4% in already lit areas from 2012 to 2016.

### Study species

*Agrotis exclamationis* (Linnaeus, 1758) (Lepidoptera, Noctuidae) is common and widespread in our study region, at least over the past 137 years. It is a nocturnal pollinator, exhibiting forewing length of 15 to 19 mm s and occurs in grasslands, parks, gardens, glades, ruderal sites, and on forest edges, rarely at clearings. It is widespread from Europe to Asia, and produces two generations from May to July, and from August to September, the latter comprising smaller individuals (Ebert, Rennwald & Bartsch, 1997). We only examined imagines from the first generation to ensure comparable traits. Relative to migratory moths, *Agrotis exclamationis* is a medium mobile species. Jones, Lim, Bell, Hill and Chapman (2016) show that males cover distances of up to 6935 m. Females deposit their eggs on host-plants (Xu, Liu & Zhang, 2013). Larvae are generalist feeders (Ebert, Rennwald & Bartsch, 1997), and may become crop and potato pests (Xu et al., 2013). Sexes can be distinguished by feathered antennae in males, and string-shaped antennae in females (Ebert et al., 1997).



**Fig. 1.** Hypothetic influence of increasing light pollution on moths' morphological traits. We expect that larger moths with relatively larger eyes and forewing length will occur at sites and in times with low levels of light pollution. With increasing light pollution, we expect a decrease in body size, relative eye size, and forewing length.

### Origin of specimens

In total, we examined 79 *A. exclamationis* (48 females; 31 males), including 37 from the city of Berlin and 41 from the federal state of Brandenburg; 54 specimens (29 females; 25 males) were museum vouchers (Museum für Naturkunde, Berlin and Naturkundemuseum Potsdam), spanning the years 1880 to 1998; 25 specimens (19 females; 6 males) were collected in 2017. Museum vouchers from Berlin were collected in parks, small green spaces, industrial areas and lakefronts. Vouchers from ruderal Brandenburg were collected around small villages and within larger towns. Museum labels mentioned that vouchers were collected with light traps. Recently collected specimens were captured manually by black light traps on 18 dry grassland sites within Berlin and two dry grassland sites in Brandenburg (June to July 2017) (see Appendix C: Table 1). We assume that museum vouchers were manually picked from light traps for the respective collections (no passive collection for ecological studies). Because our species is known to be mainly attracted by short-wavelengths (Fayle, Sharp & Majerus, 2007; Somers-Yeates, Hodgson, McGregor, Spalding & Ffrench-Constant, 2013) samples from 'white' (with a

high proportion of blue light) and 'black' lights traps (UV and blue light) should be comparable.

### Measurements

Specimens were pinned planar in drawers. Complete drawers with all specimens were scanned with a SatScan™ imaging system developed by SmartDrive Ltd., including a camera with a 0.16x telecentric lens. The camera moves along rails positioned above the drawer and captures 240 images at precise positions. These images are then 'stitched' with SatScan analyse 64 software to produce a single high-resolution image of the entire drawer (Johnson, Mantle, Gardner & Backwell, 2013). Body length, and forewing length measures were taken from these figures using the ruler tool in Adobe Photoshop (Version: CS 5.1). Standardized body length (SBL) measures were taken with modifications following Kavanaugh (1979). SBL commonly comprises head length, thorax length and abdominal length. We measured abdominal length by summing up all 10 single segment measures of the abdomen by using the maximum distance because abdomens of some vouchers were curved

to one side. For better measures of some segments that were partly covered by other segments, we used polygon lasso and magic lasso tools to uncover them. Forewing length (FWL) were measured from the anterior axillaria joint of the forewing with the thorax along the costa contact with parapteron episternale to the tip of the forewing. Horizontal diameters of the eyes were measured with a measuring ocular attached to a dissecting microscope (Leica MZ 12) (see Appendix A). Measurement errors were determined by the mean of a randomized chosen subsample of 10 specimens (accuracy was: SBL:  $\pm 0.03$  mm; FWL:  $\pm 0.06$  mm; eye diameter:  $\pm 0.03$  mm). The data used in the analyses were standardized to SBL: relative mean diameter of the left and right eye (eye diameter / SBL), and the relative mean length of the left and right forewings (FWL / SBL).

## Data classification

For categorization of ALAN levels at different sites and years, we used the “light pollution map” ([www.lightpollutionmap.info](http://www.lightpollutionmap.info)) (Light pollution map, 2019), based on satellite data from the defense Meteorological Satellite Program-Operational Linescan System (DMSP; 1992 to 2011; spatial resolution:  $5 \times 5$  km), and the Visible Infrared Imaging Radiometer Suite Day-Night Band (VIIRS DNB; 2012 to 2019; spatial resolution:  $750 \times 750$  m, see Miller et al., 2013). Especially VIIRS DNB has been shown to have sufficient resolution to identify major sources of waste light (Kyba et al., 2015). The maps based on VIIRS DNB data were used to display radiance values ( $10^{-9}$  W / cm<sup>2</sup> \* sr) for every verified moth collection site. In contrast, maps based on DMSP data are classified into light categories. The higher spatial resolution of DMSP and VIIRS DNB pixel between different years are sufficient for our analyses because they match the accuracy of the museum label data, usually given on Berlin district levels, districts usually being even larger than the spatial resolution of DMSP pixel.

For moths collected in 2017, we used absolute radiance values of their respective sampling sites. For moths collected in previous years (1880 to 2010), we calculated for each collection site the mean relative rate of ALAN increase over the years 2012 to 2019 from maps that are covered by VIIRS DNB. With these site-specific ALAN increase rates over seven years, we back-calculated the ALAN levels of former years, using time steps of seven years (see Appendix C: Table 1). To evaluate the reliability of this approach, we validated our calculated radiance values with the map based on DMSP data from 1998 to 2005. All retrospectively calculated radiance levels were within the given intervals of the DMSP light categories of the respective year.

In a next step we established our own Light Pollution Categories (LPC) of both measured and back-calculated radiance values. Category 1 ‘low’ is spanning radiance values from 0 to 0.25; category 2 ‘medium’ from 0.25 to 1.50 and category 3 ‘high’ from 1.5 to 50.0 ( $10^{-9}$  W / cm<sup>2</sup> \* sr). We

used ‘LPC’ for spatial analyses and temporal analyses for investigating effects of light pollution on a larger scale.

## Statistical analysis

For all analyses we used software of the R-Project, version 3.6.3 (R Core Team, 2020). For testing normal distribution of ‘Radiance’ values, we used Shapiro Wilk tests. For non-normally distributed data, we used Spearman correlations, testing for correlation between ‘Radiance’ and ‘Year’ for the entire study region Berlin-Brandenburg (‘Radiance’ ~ ‘Year’) to get a rough overview of the ALAN situation in the entire region; and separately for the different areas Berlin (‘Radiance Berlin’ ~ ‘Year’) and Brandenburg (‘Radiance Brandenburg’ ~ ‘Year’), respectively.

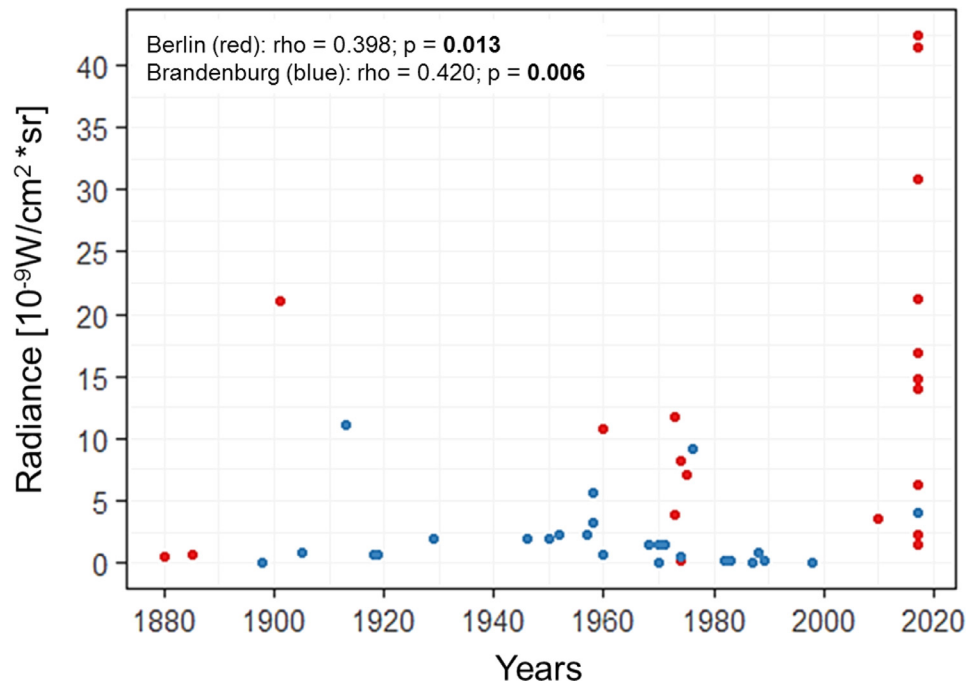
We tested distribution of our response variables (‘SBL’; ‘eye diameter / SBL’ and ‘FWL / SBL’) by visualisation via QQPlot with the R packages ‘carData’ (Fox, Weisberg & Price, 2019) and ‘MASS’ (Venables & Ripley, 2002). With normal distribution, fitting our data best, we ran linear regression models for temporal analyses. We used ‘Radiance’, ‘Year’ and ‘Sex’ as factors, tested the interaction between ‘Year’ and ‘Radiance’ (Lm = ‘Trait’ ~ ‘Year’ \* ‘Radiance’ + ‘Sex’), and did the same for testing ‘Light Pollution Categories’ (LPC) (Lm = ‘Trait’ ~ ‘Year’ \* ‘LPC’ + Sex).

For spatial analyses we used one-way analyses of variance (ANOVA), separately for sexes, by using ‘LPC’ as grouping variable (‘Trait’ ~ ‘LPC’). We used Pearson correlations, testing for correlation between ‘SBL’ and ‘Year’ and between ‘eye diameter / SBL’ and ‘Year’, both separately for males and females. For visualization, we used ggplot2 with the R-package ggplot2 (Wickham, 2016).

## Results

The Spearman correlation between ‘Radiance’ and ‘Year’ for the entire study region, Berlin-Brandenburg, was significant ( $S = 31,308$ ;  $\rho = 0.619$ ;  $p < 0.001$ ), indicating a continuous increase of light pollution over time. This correlation was equally significant for the sub-regions, although the correlations were weaker; Berlin:  $S = 5505.6$ ;  $\rho = 0.398$ ;  $p = 0.013$ ; and Brandenburg:  $S = 6664.1$ ;  $\rho = 0.420$ ;  $p = 0.006$  (Fig. 2).

We detected no significant effect of ‘Radiance’ on any of the investigated traits. However, body size differed between sexes (Lm:  $df = 74$ ;  $t = -4.070$ ;  $p < 0.001$ ) and changed over years (Lm:  $df = 74$ ;  $t = 2.402$ ;  $p = 0.019$ ). Size of both sexes was significantly positively correlated with ‘Years’ (Pearson correlation: females:  $t = 2.687$ ;  $df = 46$ ;  $R^2 = 0.368$ ;  $p = 0.010$ ; males:  $t = 2.348$ ;  $df = 29$ ;  $R^2 = 0.400$ ;  $p = 0.026$ ), i.e. body size increased over time but not in response to ‘Radiance’ (Fig. 3A). Likewise, relative eye size differed between sexes (Lm:  $df = 74$ ;  $t = 7.757$ ;



**Fig. 2.** Radiance values taken from the light pollution maps for the year 2017 ([www.lightpollutionmap.info](http://www.lightpollutionmap.info)), and back-calculated radiance values for the years 1880 to 2010 for moth collecting sites from the Berlin-Brandenburg region, Germany. Significant  $p$ -values of Spearman correlation are given in bold.

$p < 0.001$ ), and changed over years (Lm:  $df = 74$ ;  $t = -2.474$ ;  $p = 0.016$ ). Females' eye size was significant negatively correlated with 'Years' (Pearson correlation:  $t = -2.502$ ;  $df = 46$ ;  $R^2 = -0.346$ ;  $p = 0.016$ ), whereas the negative correlation in males' eye size between 'Years' was non-significant. Thus, females' relative eye size decreased over time but again, not in response to 'Radiance' (Fig. 3B). Relative forewing length did not differ between sexes and did not change over years (see Appendix B: Table 1).

We found no significant effect of 'Light Pollution Categories' (LPC) ('high', 'medium' and 'low') on any of the investigated traits in our temporal analyses. However, there was a trend for relative eye size (Lm:  $df = 74$ ;  $t = -1.949$ ;  $p = 0.055$ ), indicating smaller-eyed females in 'medium' and 'high' LPCs compared to 'low' LPCs (Fig. 4). The interaction between 'LPC' and 'Year' indicated also a trend (Lm:  $df = 74$ ;  $t = 1.988$ ;  $p = 0.051$ ), showing that increasing 'LPCs' across years have an influence on the trend of decreasing eye size (see Appendix B: Table 2). We found no significant effect in our spatial analysis. Body size, relative eye size and forewing length did not differ between areas with 'low', 'medium' and 'high' light pollution categories. This absence of any effects was detected in males as well as in females (see Appendix B: Table 3).

## Discussion

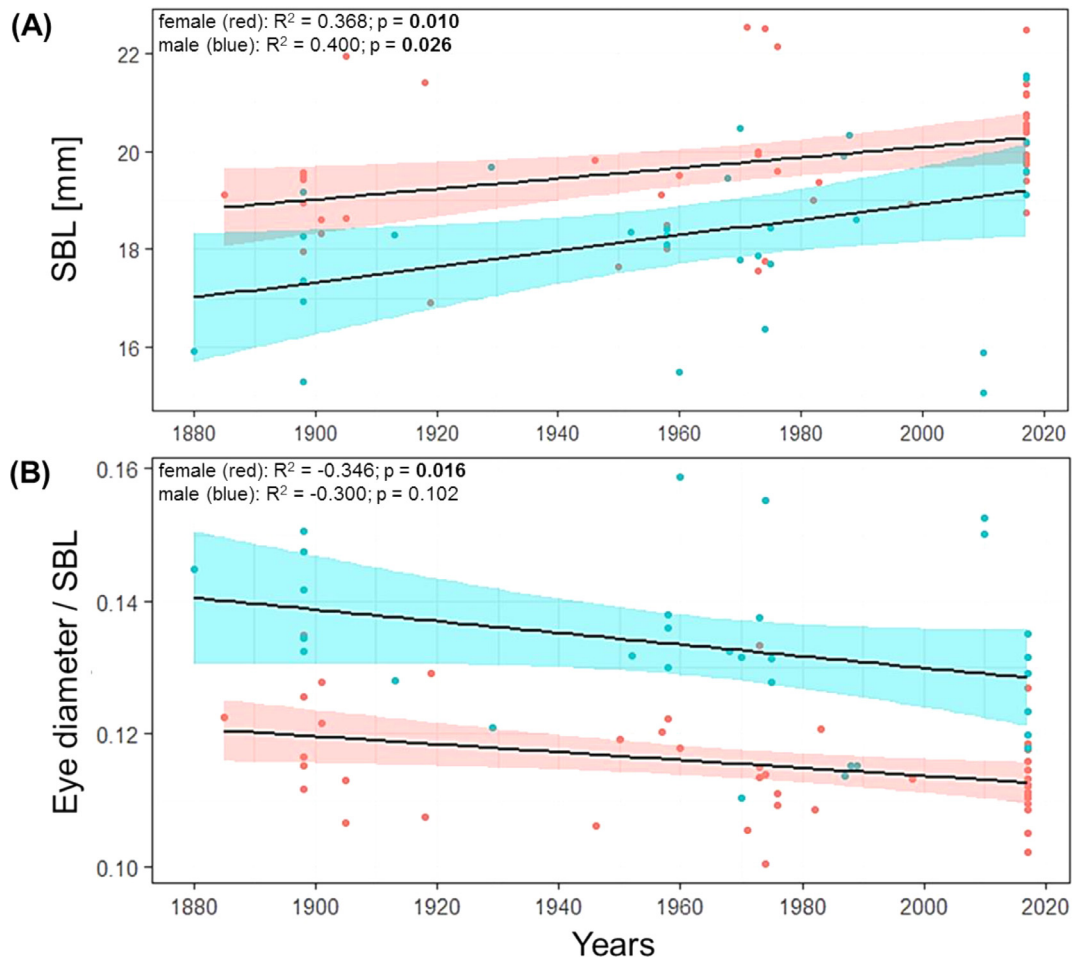
Increasing artificial light at night (ALAN) is known to have consequences on nocturnal moths, because they are

distracted by artificial light. Therefore, natural selection should favour individuals that are less impacted by ALAN (Van Langevelde et al., 2011), what could lead to intraspecific morphological trait changes.

In our study we focused on spatio-temporal changes in body size, relative eye size and forewing length in the moth *Agrotis exclamationis* in response to different ALAN levels within the Berlin-Brandenburg area, Germany. We predicted smaller-sized specimens with relatively shorter forewings and smaller eye size in areas and times with high levels of ALAN than in less impacted areas and times.

Generally, we observed that *A. exclamationis* displayed sexual dimorphism in body and relative eye size, but not in forewing length. Body size increased in both sexes, whereas relative eye size decreased only in females over the past 137 years. Both effects could not be verified as a direct response to ALAN. However, we detected a trend towards smaller eye size in females when ALAN levels increased over time. No changes were observed in forewing length in both sexes over time, and no differences occurred in any trait along the spatial gradient.

The lack of trait changes in response to increasing ALAN across space and time was unexpected and needs explanation. First, all of our specimens were captured with light traps. Thus, our specimens may have shown a pronounced flight-to-light behaviour, whereas we may have missed individuals with a reduced flight-to-light behaviour. Only a light-independent collecting method like pheromone traps, traps based on floral compounds (Tóth et al., 2010) or malaise traps (Hallmann et al., 2017) might clarify that point. However, such vouchers were not available.



**Fig. 3.** Morphological trait change in *Agrotis exclamationis* over years. (A) body size (SBL), and (B) eye diameter (eye diameter / SBL) over the years 1880 to 2017 with red or light grey (females) and blue or dark grey (males) confidence intervals and smoothed regression lines from linear models and Pearson correlation coefficients. Significant p-values are given in bold. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

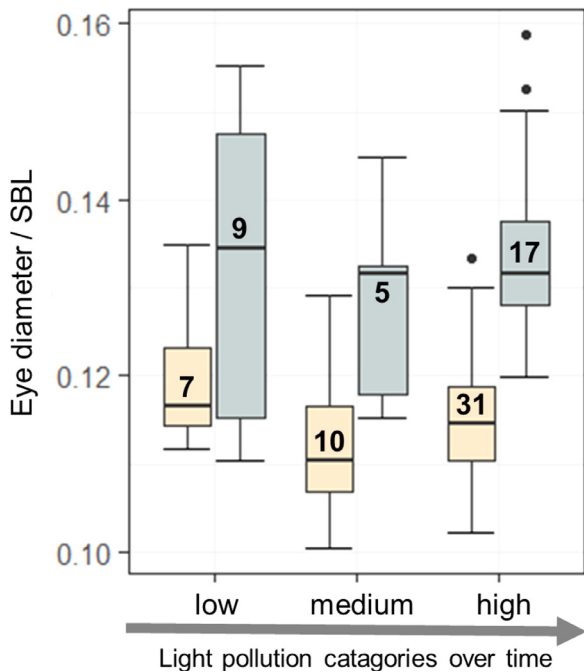
Another reason for the absence of effects in response to increasing ALAN across time might be due to our study's timeframe. Although it is known that intraspecific morphological trait change in response to human induced environmental changes may arise across relatively short timeframes in insects (Keinath et al., 2020; Van't Hof, Edmonds, Dalikova, Marec & Saccheri, 2011), and even vertebrates (Doudna & Danielson, 2015; Niemeier et al., 2020), most evolutionary processes are depending on longer times than our 137 years study period. However, in another moth intraspecific behavioural adaptations in reduced flight-to-light behaviour apparently already took place in urban areas (Altermatt & Ebert, 2016); as a consequence, morphological trait changes might follow.

A further reason for the lack of any light-driven trait changes could be due to inaccuracy of our retrospectively computed rates of ALAN. The further back the radiance calculations reached, the less certain these values might be. For instance, we based our calculations on the assumption of continuous change. However, ALAN levels were already

high during the economic boom in the 1920s (Ribbe et al., 2002b), followed by a drastic decrease during World War II. Furthermore, the spectral quality of ALAN changed over time, due to the application of different light sources (Gaston, Davies, Bennie & Hopkins, 2012; Kyba et al., 2015). Finally, the accuracy of localities on labels and thus our assignment of light intensity might have failed to reach the necessary precision, as even on a relatively small-scale light intensity can vary a lot (Kuechly et al., 2012).

An indirect hint that increasing ALAN influences our study species would be a decline in *A. exclamationis*' abundance over time in areas with high ALAN impact, and a stable population in less impacted areas. Unfortunately, such data are not available. However, Conrad, Warren, Fox, Parsons and Woiwod (2006) show a decline in *A. exclamationis* across 35 years in lit areas of Britain, and discuss increasing ALAN as one a responsible factor.

We believe that our assumptions of ALAN impacting our study species are realistic. When examining changes in



**Fig. 4.** Mean diameter of right and left eyes in relation to Standardized Body Size (eye diameter / SBL) over time (arrow) with different light pollution categories (low, medium, high) of females (reddish or light grey boxplots) and males (blue or dark grey boxplots). Numbers within boxplots give sample sizes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

response to Light pollution categories (LPC), we indeed found a trend towards smaller-eyed females in ‘medium’ and ‘high’ light polluted areas over time. These categories are larger-scaled than radiance values and could make changes more visible. We interpret this trend as a first indicator that morphological trait changes in response to ALAN are already taking place (compare Van Langevelde et al., 2011).

However, it remains to be discussed why this trend was only found in females and not in males. During our most recent sampling, more females were captured than males. This might be a hint that females are more sensitive to ALAN. In contrast, Williams (1939) could show that male *A. exclamationis* are significantly more often attracted by light traps, making this explanation unlikely. Moreover, we found a decrease in females’ eye size across time but not verifiable in response to radiance values and not in males. Male moths have larger eyes than females (Yagi & Koyama, 1963) because they are depending on visual cues for detecting females in near distance (Grant, 1987). The change of male eye size might be opposed by other selection pressures, i.e. less effective escape from predators and/or mate detection. Females in Lepidoptera are indeed known to be less dependant on their eyes for mating, instead females use vision (amongst other senses) for host-plant detection and oviposition (Bernays, 2001). *Agrotis exclamationis* is a generalist and therefore depending on high sensory capacity because they have to recognize and choose between broader

ranges on host-plants than specialists (Bernays & Weislo, 1994; Dall & Cuthill, 1997; Levins & MacArthur, 1969). Interestingly, Callahan (1957) shows that the noctuid moth *Heliothis zea* seemed to be unable to recognize host-plants for oviposition when artificially illuminated, probably because light was reflected from green plants. Thus, in areas with high ALAN levels females’ view on their host-plants might be impacted, favouring selection for females with smaller eyes which are less disrupted by ALAN. Additionally, a change of plant composition due to human-established plant species in our anthropogenically influenced study area (Sukopp & Werner, 1983; Zerbe, Maurer, Schmitz & Sukopp, 2002) could be a reason for females’ decrease in eye size probably due to a diluting effect of their native, established host-plant species.

We also predicted body size and relative forewing length to become smaller with higher ALAN levels because specimens that are more mobile may encounter and consequently become distracted by artificial light more often (Chai & Srygley, 1990; Rutowski et al., 2009; Van Langevelde et al., 2011). Our findings revealed increased body size in both sexes over time, but not in response to ALAN. We found no changes in forewing length in both sexes. Merckx, Kaiser and Van Dyck (2018) demonstrate increasing body size in macro-moths due to increasing habitat fragmentation in urban areas. Thus, over the 137 years covered in our study, increasingly fragmented habitats due to urbanisation in Berlin Antrop (2000), and intensified agriculture in Brandenburg (Cochrane & Jonas, 1999), could have opposed the potential effects of ALAN. Interestingly, it has been shown that attraction radii of streetlights overlap in most cases, building barriers for moths (Degen et al., 2016). Therefore, ALAN might have increased the fragmentation of nocturnal habitats, also in our study area, limiting moth dispersal, and thus, indirectly inducing changes in body size but not in relative forewing length.

Our results revealed that trait and sex-dependent changes in *A. exclamationis* over the past 137 years in the Berlin-Brandenburg region took place. However, these changes could not be directly linked to increasing ALAN. Nevertheless, we assume trait changes to have been indirectly induced by ALAN as a result of habitat fragmentation (Degen et al., 2016) and females’ changed perception of host-plants (Callahan, 1957). However, we found a trend of sex-dependant changes in eye size which may be directly related to different levels of light pollution, and thus a first sign of light pollution driving morphological trait change.

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## Declaration of Competing Interest

None.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.05.004.

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