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Artificial light at night increases the nighttime feeding of monarch butterfly caterpillars without affecting host plant quality

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A B S T R A C T

Most research on the effects of artificial light at night (ALAN) on animal behaviour focuses on nocturnal species. In addition, there are few studies on the effects of ALAN on the feeding behaviour of herbivores or how such behavioural changes affect herbivore performance. In this study, we tested whether ALAN has direct effects on the feeding frequency and performance of the larvae of the monarch butterfly (*Danaus plexippus*), a species in which adults are diurnal but larvae exhibit little diel rhythm in feeding activity. We also tested for effects of ALAN on the growth, nutritional quality, or anti-herbivore defences of this herbivore's primary host plant in North America, common milkweed (*Asclepias syriaca*). There was no evidence that ALAN affected the growth, nutritional quality or defensive traits of the host plant. However, at night, the feeding frequency of larvae exposed to ALAN was two times higher than in larvae that were not exposed to ALAN. Despite this effect on feeding frequency, ALAN had no significant effects on larval development time (days from second instar to pupation) or pupal mass. Our study highlights that ALAN can have strong impacts on the feeding activity patterns of herbivorous insects and that these impacts are not limited to nocturnal species.

Introduction

To the detriment of many species, and perhaps to the benefit of some, 23% of the Earth's land surface (excluding Antarctica and the High Arctic) was enveloped by artificial light at night (ALAN) as of 2016 (ALAN; Falchi et al., 2016). Effects of ALAN on the foraging behaviours of predators, such as shifts in the diel timing of foraging and concentrating foraging in areas where prey have been attracted by ALAN, have been widely documented across a wide variety of taxa including birds, mammals, and arthropods (reviewed in Gaston et al., 2017). Much less is known about effects of ALAN on the feeding activities of herbivores or how this influences their performance.

In herbivorous insects, ALAN can affect performance or abundance either directly through effects on feeding activity (van Langevelde et al., 2017) or indirectly through effects on host plants (Bennie et al., 2015; Grenis & Murphy, 2019). van Langevelde et al. (2017) showed that ALAN directly reduced the nighttime feeding frequency of the larvae of four nocturnal moth species. In contrast, Grenis and Murphy (2019) found that ALAN decreased the performance (body mass) of moth larvae indirectly by reducing host plant quality. As the effect of ALAN on photosynthesis is likely minimal due to its low intensity relative to sunlight, plants are thought to respond to ALAN mainly through processes regulated by photoreceptors (Bennie et al., 2015). ALAN has been shown to influence a variety of plant characteristics that could impact herbivores (e.g., biomass, flowering, toughness; Bennie et al., 2015; Grenis & Murphy, 2019). However, we are unaware of conclusive evidence that ALAN affects anti-herbivore defences.

Here, we examine effects of ALAN on the feeding activity of the monarch butterfly (*Danaus plexippus*) and the size, nutritional quality, and anti-herbivore defences of its primary host plant in eastern North America, common milkweed. Though monarch butterfly adults are diurnal, its larvae display no diel rhymicity in feeding rates under constant temperature (Niepoth et al., 2018). The species engages in long-distance migration, breeding throughout the United States and southern Canada and overwintering in isolated colonies in California and Mexico. The overwintering populations have been declining for multiple decades; however, population growth during summer may be counterbalancing these declines (Crossley et al., 2022). Common milkweed is considerably less abundant than it was prior to widespread use of agricultural herbicides and glyphosate-tolerant crops (Pleasants & Oberhauser, 2013; Stenoien et al., 2018). Now largely excluded from agricultural fields, common milkweed likely encounters ALAN

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throughout more of its range, as it often grows along roadsides and in other disturbed habitats (Kaul & Wilsey, 2019). Exposure of monarch larvae to ALAN has likely increased in parallel with the exposure of common milkweed, its primary host plant in this system.

Common milkweed is well defended from herbivory by toxic secondary metabolites, trichomes, and latex (Agrawal, 2017). The species has been shown to have decreased latex, content of toxic cardenolides, leaf toughness and trichome defences when shaded from natural sunlight (Agrawal et al., 2012). This indicates that defensive traits, which could theoretically affect herbivore performance and preference, can be impacted by light regimes. Although monarch caterpillars have evolved responses to milkweed defences, plants with weaker defences favour increased larval performance (Agrawal et al., 2012).

We hypothesized that ALAN directly affects the performance of monarch larvae by inducing a change in the insects' nighttime feeding frequency or indirectly by affecting the growth, nutritional quality, or anti-herbivore defences of its host plant. We experimentally tested whether ALAN, at an intensity typical under streetlights, affects several attributes of common milkweed, the dominant host plant for monarch larvae in eastern North America. We then tested whether ALAN of the same intensity affects the feeding frequency, during nighttime and daytime, and performance of monarch larvae. These experiments were carried out in a greenhouse in which plants were exposed to ALAN from broad-spectrum white LED light or were unlit.

Materials and methods

Effects of ALAN on host plants

We studied the effects of ALAN on the growth, nutritional content, and antiherbivore defences of common milkweed in a greenhouse experiment at the University of Virginia's Blandy Experimental Farm (Boyce, VA, USA) in 2018. Young plants ($<$ 1 year old) were obtained from a local nursery and planted individually into 2.5 L pots. The plants were placed either in locations within the greenhouse where ALAN was added or locations that were unlit (i.e., control locations). For each location receiving ALAN, a single LED was hung 50 cm above the surface of the soil within the pots. Artificial light at night was added using broad-spectrum 'white' LEDs (5000 K, 11 W). Dimmer switches were adjusted to approximate light intensity typically found at ground level under roadside streetlights ($\sim$30 lx; Bennie et al., 2016). At midnight, mean light intensity at soil level was 33.9 $\pm$ 6.0 (mean $\pm$ SE) lx in the locations where ALAN was added, whereas light intensity was 0.05 $\pm$ 0.02 lx in for plants in the unlit locations. Artificial light at night was added from civil dusk to civil dawn each night of the experiment. Each night, opaque black plastic partitions, which extended from the benchtops to 90 cm above the benchtops, were used to prevent the artificial light from trespassing between locations. The partitions were taken down at civil dawn each day to prevent the shading of sunlight. This lighting regime was maintained for 36 d (11 June-16 July 2018) except for one night due to a power outage. We felt this length of time was sufficient to affect the traits of common milkweed, particularly its inducible defences. Latex and cardenolides exist as both constituent and inducible plant defenses in common milkweed, and these traits are expressed at higher levels in response to bursts of the hormone jasmonic acid (Agrawal et al., 2014), which can be triggered by extended photoperiods in other species. Departure from natural photoperiods represents a major alteration to a plant's abiotic environment and has been found to stimulate the jasmonic acid pathway in *Arabidopsis* in a 21-day experiment (Cagnola et al., 2018).

The experiment was conducted using a randomized block design to account for potential differences in abiotic conditions experienced by the plants based on their position within the greenhouse. For example, exhaust ventilation fans embedded in the northern wall of the greenhouse may have subjected plants nearby plants to stronger air currents than plants placed farther from that wall. Each treatment level (ALAN or unlit control) was replicated in each of five blocks ($n = 5$ per treatment). Each block consisted of a pair of locations, one on a bench on the west side of the greenhouse room and one on a bench on the east side of the room, at a given distance (1.5 m, 3 m, 4.5 m, 6 m, or 7.5 m) from the southern end of the room. Within each block, ALAN was applied at random to one of the two locations, while the other location was unlit to act as a control. Thirty-two plants were placed in each block, 16 per location placed in a tightly packed, roughly circular formation. Sixteen plants were removed from the experiment during weeks two and three of the experiment because they became infested with aphids and/or thrips and a natural pesticide (neem oil) was applied to the plants to help control the infestations. During weeks three to four of the experiment, eight to ten plants per location were selected at random and removed for use in a separate experiment. At the conclusion of the experiment, two to six plants remained per location. Because response variables were averaged across all plants within a location to avoid pseudoreplication, removals of individual plants had no effect on sample size, which was the same for all response variables ($n = 5$ per treatment).

Twenty-five days after the start of the experiment, we obtained measurements of anti-herbivore defences (latex exudation and trichome density) and water content through destructive sampling of one randomly selected plant from each treatment in each block. These destructively sampled plants were removed from the experiment. Following Rasmann et al. (2009), we measured latex exudation from the most recently fully expanded leaf by cutting off five mm of the leaf tip with scissors and allowing the latex to run for 10 s onto a 1-cm^2 section of filter paper of a known mass. The filter paper was dried at room temperature for 2 d and weighed to obtain the dry mass (g) of the latex. Next, using the same leaf, we obtained an estimate of trichome density. A 28-mm^2 disc was removed from the leaf using a hole punch. We photographed the disc under a dissecting microscope and used ImageJ software (Abramoff et al., 2004) to sharpen the images and correct for shadows. We then counted the number of trichomes within a 2 mm^2 area on each leaf disc (Colvin et al., 2013). Water content was measured using the opposite leaf in the same leaf pair. This leaf was cut, weighed, dried (2 d at 60 °C), and reweighed.

The effects of ALAN on plant size (height, total leaf area, basal stem diameter) and leaf chlorophyll content, the latter used as a proxy for nitrogen content (Evans, 1989; Luo et al., 2019), were assessed at the conclusion of the experiment. Total leaf area was estimated as $\sum_1^k 2A_i$ where k was the number of leaf pairs present, and A_i was the area of one leaf in leaf pair i. The area of an individual leaf (A_i) was estimated as (length $\times$ width) / 2 (Züst et al., 2015). Because this method assumes that the leaves in each leaf pair are approximately the same size, measurements were taken from both leaves in cases where paired leaves exhibited obvious size differences. Chlorophyll content index (CCI) values were obtained using a chlorophyll content metre (CCM-200plus, Opti-Sciences, Hudson, NH, USA), with measurements taken at the tip of the most recently fully expanded leaf on either side of the leaf vein. While the plant size variables were measured starting in the first week of the experiment, CCI was sampled consistently beginning in the third week. Infrequent measures of the CCI prior to week three were not analysed.

Effects of ALAN on herbivore feeding behaviour and performance

In 2019, two greenhouse experiments were conducted, one to examine how exposure of monarch larvae to ALAN affected the feeding frequency of larvae during nighttime and daytime, and another to examine effects of ALAN on larval performance. The plants were not exposed to ALAN prior to a trial to minimize the potential for ALAN-induced changes in plant characteristics so that changes in larval feeding and performance could be attributed, to the maximum extent possible, to direct effects of ALAN on larval feeding behaviour. The larvae also had no exposure to ALAN prior to a trial. During the trials, ALAN was manipulated in the same manner as in the 2018 experiment described above; we used the same lighting equipment and light-blocking partitions arranged in the same locations, recreating the randomized block design with ALAN or unlit control treatments applied at random to one of the two locations within each of the five blocks ($n = 5$ per treatment).

Effects of ALAN on feeding frequency were examined during four different trials (June 27–30, July 3–6, July 9–12, and July 21–24) with trial treated as a temporal block. On the first day of a trial period, two nylon mesh butterfly cages (41 × 42 × 72 cm; Educational Science, League City, TX, USA) were placed into each of the 10 locations (five blocks × two treatments) and each cage was stocked with a potted common milkweed and a second- or third-instar larva. To achieve independence amongst trials, new plants and larvae were used in each trial. The plants for these experiments were grown in the spring of 2019 from seeds sewn into potting soil (Sungrow Horticulture Professional Growing Mix; Sungrow Horticulture, Agawam, MA, USA). Three weeks after the seeds were sown, we transplanted 160 seedlings individually into 2.5 L pots. The monarch larvae were obtained from Monarch Watch (University of Kansas, Lawrence, KS, USA). Monarch Watch raised larvae under a 12-h light/12-h dark cycle and kept parental adults under a 10-h light/14-h dark regime. Prior to the feeding trials, we fed the larvae leaves of common milkweed collected from plants growing in early successional habitats at Blandy Experimental Farm.

To assess feeding frequency during daytime and nighttime, we observed each larva repeatedly during a trial, each time recording whether or not it was feeding. These observations were made at 3 h after sunrise, 3 h before sunset, 3 h after sunset, and 3 h before sunrise, for a total of six daytime and six nighttime observations over the course of three complete diel periods. Following van Langevelde et al. (2017), we used an infrared-sensitive camcorder (Sony, DCR-SR85) to observe larvae in nighttime darkness. Feeding frequency was calculated as the number of times a larva was observed feeding divided by the number of times observed. An observation was excluded from this calculation if the larva was moulting because larvae do not feed while moulting, and likewise if a larva was found dead. In addition, during one of the feeding trials, data from one of the blocks was not used because the lighting used to add ALAN failed.

To assess effects of ALAN on performance, two butterfly cages were placed into each of the 10 locations (five blocks × two treatments) and each cage was stocked with a potted common milkweed and a second-instar larva. The time since these larvae reached the second instar was not known and may have varied amongst individuals. Half of the cages were exposed to ALAN while the other half were unlit according to a randomized block design. Performance was assessed based on the number of days needed to develop into pupae and pupal mass. Due to sexual dimorphism in body mass, we reared the pupae to adulthood to determine their sexes.

To evaluate whether the effects of ALAN on larval feeding behaviour or performance could be confounded by changes in air temperature caused by heat produced by the LEDs, we measured mean temperature within the mesh cages from sunset to sunrise at a height of 35 cm above the cage floor using two DS1922L Thermochron temperature loggers (OnSolution Pty Ltd, Bualkham Hills, Australia), each set to record temperature every 5 min. Within a given block, temperatures were recorded simultaneously within one cage exposed to ALAN and one cage not exposed to ALAN for a period of one to three nights. The temperature loggers were then moved successively between blocks until all blocks were sampled.

Data analysis

To avoid pseudoreplication, response variables were averaged across all plants within each of the locations ($n = 5$ per treatment) in the greenhouse prior to data analysis. Effects of ALAN on the size (height, basal stem diameter, total leaf area), defences (trichome density, latex exudation), and nutritional quality (leaf water and chlorophyll content) of common milkweed were examined according to a randomized block design using ANOVAs. Block was modelled as a fixed effect instead of as a random effect, due to its low number of levels (five) because inaccurate estimates of the variance of random effects that have few levels can plague mixed-effects modelling (Arnqvist, 2020). To normalize the ANOVA model residuals and to improve heterogeneity of variance, plant height, basal stem diameter, total leaf area, latex exudation, and the CCI were Box-Cox transformed using exponents (λ) of −0.5, −2.03, 0.4, −0.32, −0.58, respectively.

The herbivore feeding behaviour and performance response variables were also averaged across the larvae within each replicate greenhouse location ($n = 5$ per treatment). We assessed the effects of ALAN on the means of frequencies of larval feeding during nighttime and daytime according to a randomized block design using ANOVA models. In addition to blocking for location within the greenhouse, we included trial number (1–4) in the ANOVA models to block for temporal variation. Effects of ALAN on performance variables (development time and pupal mass) were assessed according to randomized block design using ANOVA models, with the blocks representing the five paired locations within the greenhouse. The sexes of the two larvae in each greenhouse location (both male, both female, or male and female) was included in these models as a fixed effect. To assess whether heat produced by the LEDs that were used to add ALAN might have influenced larval behaviour or performance, we tested for potential effects of ALAN on mean nighttime temperatures using an ANOVA with block (greenhouse location) as a fixed effect. Blocks were included as fixed effects due to the low number of levels in each group. Daytime and nighttime feeding frequencies were Box-Cox transformed prior to analysis to improve normality using exponents (λ) of 0.52 and 0.24, respectively. For both daytime and nighttime feeding frequencies, 0.1 was added to all observations prior to transformation due to the presence of zeros. All analyses were carried out in the R computing environment (R Core Team, 2022).

Results

Effects of ALAN on host plants

There were no significant effects of ALAN on our indices of plant size (Fig. 1, see Appendix A, Tables A1–A3, height, $F_{1,\,4} = 0.016$, $P = 0.907$; basal stem diameter, $F_{1,\,4} = 0.237$, $P = 0.652$; total leaf area, $F_{1,\,4} = 0.061$, $P = 0.816$), anti-herbivore defences (Fig. 1, Tables A4 and A5, trichome density, $F_{1,\,4} = 0.081$, $P = 0.790$; latex exudation $F_{1,\,4} = 0.142$, $P = 0.725$), or plant nutritional quality (Fig. 1, Tables A6 and A7, leaf water content, $F_{1,\,4} = 1.048$, $P = 0.364$; CCI, $F_{1,\,4} = 0.258$, $P = 0.638$).

Effects of direct ALAN exposure on larval feeding frequency and performance

Artificial light at night caused a two-fold increase in the frequency of feeding at night (Fig. 2A, Table A8, $F_{1,\,29} = 6.891$, $P = 0.014$). As the frequency of moulting (proportion of observations in which larvae were moulting) at night under ALAN (0.22) was nearly identical to frequency of moulting at night in the unlit controls (0.24) the effect of ALAN on feeding frequency was likely not influenced by changes in moulting frequency. During daytime, the feeding frequency of larvae exposed to ALAN was also higher than for larvae in the unlit controls (Fig. 2B), but not significantly so (Table A9, $F_{1,\,29} = 0.817$, $P = 0.374$). There were no significant effects of ALAN on two measures of performance, days to develop from second-instar larvae to pupae (Fig. 3A, Table A10, $F_{1,\,2} = 0.036$, $P = 0.867$) or pupal mass (Fig. 3B, Table A11, $F_{1,\,2} = 4.727$, $P = 0.162$). Development time ($F_{2,\,2} = 0.465$, $P = 0.683$) and pupal mass ($F_{2,\,2} = 2.514$, $P = 0.285$) were not significantly affected by gender composition (both male, both female, or one male and one female). Nighttime temperatures within the insect cages were not significantly

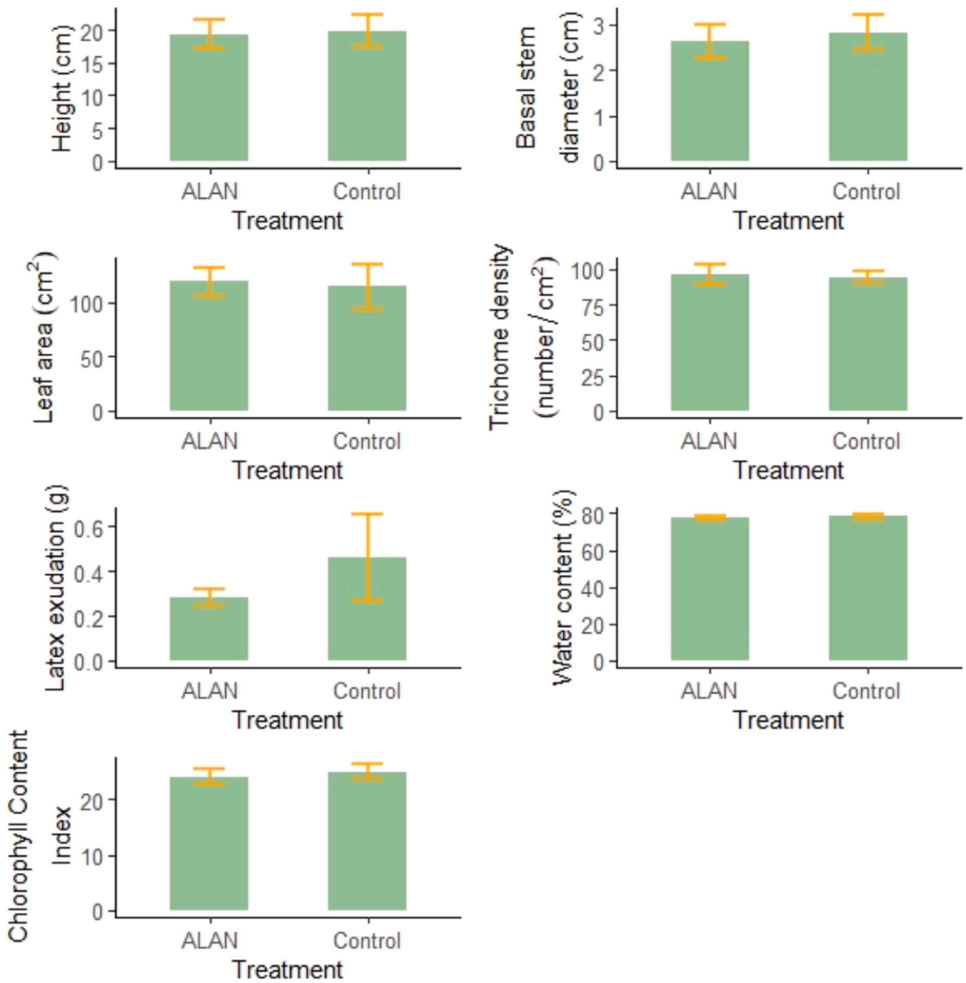

Fig. 1. The effects of artificial light at night (ALAN) on the height, total leaf area, basal stem diameter, latex exudation, leaf trichome density, leaf chlorophyll content index, and water content of common milkweed (means ± 1 SE).

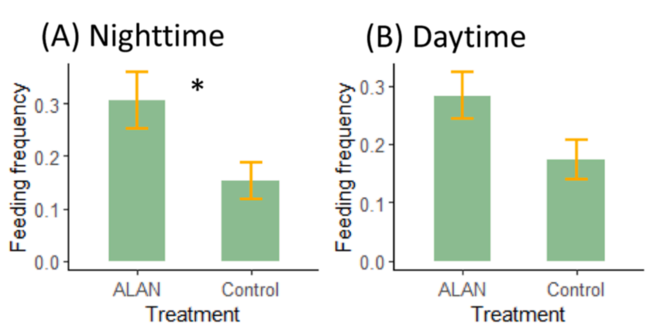

Fig. 2. The effects of artificial light at night (ALAN) on the frequency with which monarch butterfly larvae were observed feeding on common milkweed during (A) nighttime and (B) daytime (means ± 1 SE). Significant effect of ALAN at the α = 0.05 level is marked with an asterisk (*).

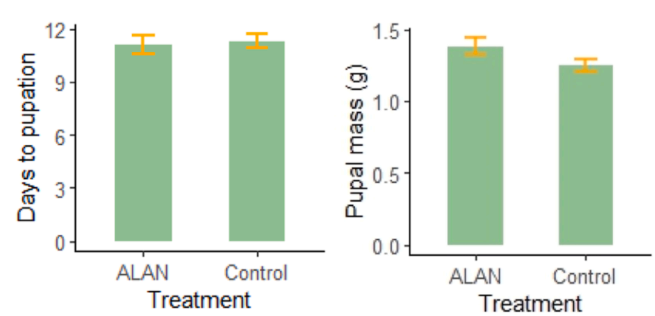

Fig. 3. The effects of artificial light at night (ALAN) on the number of days required for second-instar larvae to pupate and pupal mass (means ± 1 SE).

affected by the addition of ALAN (Table A12, $F_{1,\,4} = 0.221$, $P = 0.663$); on average, the mean nighttime temperature was only 0.04 °C warmer under ALAN than in the unlit controls.

Discussion

Most studies of effects of ALAN on the behaviour or performance of insects have focused on nocturnal insects (Desouhant et al., 2019). van Langevelde et al. (2017) found that ALAN caused a reduction in the feeding frequency of the larvae of nocturnal moths, potentially contributing to observed regional declines in moths (van Langevelde et al., 2018). In contrast, for a species in which adults are diurnal but larvae show little diel rhythmicity (Niepoth et al., 2018), we found that the feeding frequency of larvae at night was two times higher under ALAN than under unlit conditions (Fig. 2A). This increased feeding rate under ALAN was likely due to a direct effect of ALAN on larval behaviour, and not the result of an effect of ALAN on plant quality or defences, because the plants in this experiment were not exposed to ALAN prior to the feeding trials. Large differences in diel activity patterns between different life stages (e.g., between larvae and adults) of the same insect species have been observed across many insect taxa (e.g., Lepidoptera, Phasmatodea, Orthoptera, Ephemeroptera, Odonata), including increasing or decreasing rhythmicity in later life stages and changes in peak activity times (Harker, 1973). Therefore, it is possible that the impacts of ALAN on the diel timing of insect behaviours shift between life stages in such taxa.

Our experiment examined the behavioural responses of monarch caterpillars to ALAN in the absence of predators and parasitoids. In the field, early-instar monarch caterpillars are preyed upon by a variety of arthropod predators (Prysby, 2004), while relatively few predator species will attack late-instar caterpillars (Rafter et al., 2013). Under ALAN, predation risk for caterpillars might increase at night because of increased local abundance of predators due to positive phototaxis and the extension of foraging of diurnal predatory insects into nighttime hours (Deitsch & Kaiser, 2023; Mcmunn et al., 2019). A field experiment in which ALAN is manipulated and the behaviours of monarchs and predators are observed is needed to determine the effects of ALAN on the diel rhythms of monarch behaviour in the presence of predators.

We found no evidence that ALAN-induced increases in feeding frequency affected larval performance based on the speed of development and pupal mass. For monarch butterfly larvae, increased feeding does not necessarily lead to increased fitness as it can increase exposure to natural enemies, energetic costs associated with feeding and digestion, and exposure to milkweed latex and its toxic cardenolides (reviewed in Lavoie & Oberhauser, 2004). While ALAN had no discernible effects on larval performance in our experiment, photoperiod has been shown to affect the number of degree-days required for development from egg to adult in monarchs (Goehring & Oberhauser, 2002). Furthermore, ALAN has been shown to negatively affect circadian-clock mediated migratory behaviour of adult monarchs (Parlin et al., 2022). Given the life stage-specific effects of light on behaviour and development, and the long-distance migrations of adult monarchs, discerning the overall impact of ALAN on monarch fitness may require a combination of multi-generational controlled experiments and studies of field populations across large spatial and temporal scales.

Some studies have shown indirect effects of ALAN on the performance or abundance of herbivorous insects that were mediated by the responses of plants to ALAN (Bennie et al., 2015; Grenis & Murphy, 2019). Here, ALAN had no significant impact on the growth, quality, or defences of common milkweed (Fig. 1), the dominant host plant of monarch larvae in North America. A previous field experiment, however, of similar duration (4 weeks) but using slightly higher intensity ALAN ($\sim$50 lux) showed positive effects of ALAN on the growth of common milkweed (Hey et al., 2020). Whether exposure of common milkweed to higher-intensity ALAN or to ALAN over a longer period would lead to indirect effects on the behaviour or performance of monarch larvae is not yet clear.

Few studies have examined effects of ALAN on the feeding activity patterns of herbivores. van Langevelde et al. (2017) demonstrated that ALAN can affect the nighttime feeding frequency of an herbivorous insect, identifying this as a potential mechanism underpinning a long-term decline of nocturnal moths. Our findings on the monarch butterfly complement those results by suggesting that effects of ALAN on the feeding of herbivorous insects likely extend beyond nocturnal species.

Data availability

The data supporting the results are available upon request.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.07.007.

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