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Light pollution at night impacts monarch butterfly growth and performance

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Abstract

Artificial light at night (ALAN) can be an anthropogenic stressor, yet its effects on wildlife, especially diurnal insects, remain poorly understood. We test how ALAN influences larval growth, development, and performance of monarch butterflies (*Danaus plexippus*) reared on two host milkweed species (*Asclepias syriaca* and *A. incarnata*). Field experiments with four cohorts over 2 years revealed that exposure to ALAN from white LED streetlights consistently increased caterpillar growth rates by nearly 16% and shortened larval development time, resulting in an 8% increase in adult fresh mass across both plant species. Nonetheless, ALAN had little effect on wing loading (fresh mass to wing surface area) or adult dry mass. Host plant interacted with ALAN to impact wing morphology: butterflies reared on *A. syriaca* had 7% larger wings under ALAN, while those on *A. incarnata* were not affected. Seasonality profoundly shaped monarch life history traits, with the migratory generation developing in late summer (August–September) exhibiting slower growth, extended developmental periods, and emerging with 44% less body mass and 30% reduced wing loading capacity compared to early summer (June–July) breeding generations. Finally, a path analysis revealed that ALAN enhanced larval growth, on par with the effects of feeding on *A. syriaca* compared to *A. incarnata*, increasing fresh mass and wing size by accelerating investment in early development. Our findings underscore that light pollution at night alters the entire developmental trajectory of these holometabolous insects, highlighting its strong capacity to reshape insect life histories in the Anthropocene.

KEYWORDS
Anthropocene, anthropogenic stressors, artificial light at night (ALAN), caterpillar development, *Danaus plexippus*, plant–insect interactions

INTRODUCTION

Sunlight, as well as the absence of light at night, is critical for synchronizing the circadian rhythms of most animals. However, life in the Anthropocene is a new era in which over a quarter of the earth's surface is covered by artificial light at night (ALAN) (Hölker et al., 2010). ALAN is a potential threat to biodiversity because it

transcends all ecosystems, from terrestrial to aquatic, and alters the physiology, life history, and performance of organisms across trophic levels (Gaston et al., 2015; Longcore & Rich, 2004; Marangoni et al., 2022; Miller & Rice, 2023; Sanders et al., 2021). Insects—particularly holometabolists like Lepidoptera—may be especially susceptible to ALAN because exposure can independently affect both their larval and adult stages. Furthermore, exposure as larvae may modify adult morphology, size, and performance (Blanckenhorn, 2000; Davis, 2014; Flockhart, 2017; Nylin & Gotthard, 1998; Soule et al., 2020), compounding effects across life stages (Boyes et al., 2021a; Johnson et al., 2014).

While the effects of ALAN on nocturnal insects are well documented (Bolliger et al., 2022; Boyes et al., 2021b; Owens et al., 2020; Owens & Lewis, 2018; Van Doren et al., 2017; Westby & Medley, 2020), its impacts on diurnal insects remain understudied (Desouhant et al., 2019). Meta-analyses suggest that diurnal species may experience greater physiological shifts in their growth, reproduction, and fitness than nocturnal species under ALAN (Bennie et al., 2015; Sanders et al., 2021; Van Geffen et al., 2015). For example, ALAN has been shown to alter the photoperiod perception of diurnal organisms, extending their daytime activities, such as foraging (Giavi et al., 2021; Haynes et al., 2023), oviposition (Daufel et al., 2023; Honnen et al., 2019), and migration (Owens & Lewis, 2018; Parlin et al., 2022). Given the rapid decline of insects in recent decades (Boyes et al., 2021a; Grubisic et al., 2018; Van Langevelde et al., 2018), it is crucial to understand how widespread anthropogenic stressors, such as ALAN affect the growth, development, and performance of insects—and how these effects may be shaped by varying abiotic and biotic factors, including seasonality and host plant species (Grenis & Murphy, 2019).

Here we test how exposure to realistic levels of ALAN during early developmental stages influences the growth and performance of the monarch butterfly *Danaus plexippus*. We selected the monarch because it is a well-established model organism for studying the plasticity of insect physiology across host plant species (Agrawal, 2017; Pocius et al., 2017) and seasonality (Altizer & Davis, 2009). Additionally, numerous studies have documented the impacts of other anthropogenic stressors—such as rising temperatures (Couture et al., 2015; York & Oberhauser, 2024; Zylstra et al., 2021), habitat degradation (Boggs & Freeman, 2005; Brower et al., 2012), and pesticide exposure (Hastings et al., 2026; Olaya-Arenas et al., 2020) on this iconic species of conservation concern. These impacts occur across all life stages, illustrating the delicate relationship between larval performance and adult morphology in the Anthropocene. For example, under warming temperatures, caterpillars develop faster, resulting in a decline in body mass (York & Oberhauser, 2002), wing size (Soule et al., 2020), and subsequent wing loading (weight-to-wing surface area ratio) (Altizer & Davis, 2009; Dingle, 1972; Ebada et al., 2023; Soule et al., 2020; Warham, 1977), ultimately curtailing the performance of butterflies experiencing climate stress.

In this study, we examine (1) the direct effects of ALAN on larval growth, development, and adult traits including body mass, wing surface area, and wing loading, (2) whether the host plant species modulates the impact of ALAN on these performance metrics, and (3) how resident butterflies in the summer may respond to ALAN compared to migratory butterflies later in the fall. We reared caterpillars under either white LED light (ALAN) or control (natural light at night) on *A. incarnata* or *A. syriaca* across four summer generations (June–September 2023, July–August 2024). We selected the two host plant species because they co-occur regionally and are both utilized by monarchs, but vary in their intensities of defense: *A. syriaca* contains higher levels of chemical and physical defenses than *A. incarnata* (Agrawal & Fishbein, 2008; Malcolm et al., 1989). Additionally, although they both can occur along roadways with streetlights (Cariveau et al., 2019; Gaston et al., 2021; Hey et al., 2020; Nichter & Gregory, 2018), *A. syriaca* is much more common in such sites, and much more heavily utilized by monarchs, setting up a contrast between two available hosts with different qualities and likelihoods of encounter.

We also explored the effects of ALAN across seasons, as eastern monarchs are known for their two distinct nonmigratory and migratory generations that display differences in their growth, wing morphology, and performance (Altizer & Davis, 2009; Davis et al., 2012; Ebada et al., 2023; Freedman & Dingle, 2018). Separately, previous research has shown that ALAN can interfere with the feeding of (nonmigratory) caterpillars (Haynes et al., 2023) and the navigation of migratory adults (Parlin et al., 2022). However, the extent to which developmental exposure to ALAN may affect their size and wing morphology, especially across migratory and nonmigratory generations, is unknown.

We hypothesized that ALAN would accelerate growth, shorten larval duration, and decrease adult body mass (Haynes et al., 2023; Loewy et al., 2013; Willmott et al., 2018). We also expected that their wings would display a developmentally plastic response to ALAN, with forewing length and overall surface area of the wings decreasing under ALAN, as mass and wing surface area are known to be positively correlated (Flockhart, 2017). We hypothesized that the effects of ALAN on monarch

development would vary depending on the milkweed species consumed (*A. syriaca* or *A. incarnata*), with monarchs exhibiting greater sensitivity to ALAN when reared on *A. syriaca*—a species known to contain higher cardenolide concentrations, higher densities of trichomes, and more latex exudation (Agrawal & Fishbein, 2008; Faldyn et al., 2018; Prouty et al., 2021). Finally, we combined our results across 2 years, multiple generations (summer and fall), and both host plants in a path analysis to understand how ALAN may reshape the development, life history, and performance of monarch butterflies.

MATERIALS AND METHODS

Plant growth

A. incarnata seeds were sourced from Joyful Butterfly (Blackstock, SC, USA), and *A. syriaca* seeds were locally collected in Ithaca, NY. Seeds were germinated in between moist paper towels in Petri dishes (Agrawal et al., 2014), planted in 1180 mL pots, and kept in three 100-square-foot walk-in chambers programmed to 14-h of light (28 μmols/1512 lux): 10 h of dark cycle. All plants were fertilized with Jacks All Purpose 20-20-20 fertilizer (Allentown, PA, USA) and sprinkled with *Amblyseius cucumeris* mites weekly to preventatively control thrips. *A. syriaca* and *A. incarnata* pots were randomized and evenly distributed within the growth chamber, experiencing the same pest-free growing conditions. Potted plants were moved to shade tents in the field 7 days prior to the experiment to adjust to the local climatic conditions (Appendix S1: Table S1).

Common garden set-up

We arranged six to eight 4 × 4 × 6 ft (1.2 × 1.2 × 1.6 m) mesh cages 30 feet (9.14 m) apart in a transect at Cornell ecological field sites (Year 1: 42.503274, −76.467617, Year 2: 42.443962, −76.501884; Appendix S1: Figure S2). We then assigned every other cage in the transect to have a white solar LED light shining ~7 lux of light each night (LED Lighting Solutions 6-Watt Flood Light; Appendix S1: Table S1, Figure S2). We selected this lux to simulate the ALAN levels we recorded under LED streetlights in Central, NY. The lights were placed 178 cm above ground level, 30 cm away from the mesh cages. We set one HOBO pendant temperature/light logger (Onset model MX2202, Bourne, MA, USA) 15 cm above the ground in the center of each cage to record the light (lux) and temperature (in degrees Celsius) every hour. We used the HOBO loggers to confirm that there was no light spillover from the ALAN cages into the control cage (which received 0 lux of light at night; Appendix S1: Table S1) and ensured that there was no difference in day/night temperatures between the two light treatments throughout the experiment (Appendix S1: Table S1, Figure S1).

Experimental design

We conducted two common garden experiments under experimental white LED light (ALAN; ~7 lux) and control (natural light at night: ~0 lux) conditions across three cohorts of butterflies between June 19, 2023 and September 11, 2023 (Year 1) and one cohort from July 24–August 30, 2024 (Year 2). Cohort 1 contained six cages (three control and three ALAN) and 10 *A. incarnata* plants per cage (60 plants total). Cohorts 2 and 3 contained eight cages (four control and four ALAN) with five pots of *A. incarnata* and five pots of *A. syriaca* (totaling 80 plants per cohort—40 *A. syriaca* and 40 *A. incarnata*; Appendix S1: Figure S2). Lastly, Cohort 4 contained eight cages (four control and four ALAN) with eight *A. syriaca* plants per cage, resulting in 64 plants (32 plants per treatment).

Butterfly rearing

We sourced monarch eggs from the eastern monarch population through Monarch Watch (Lawrence, KS, USA), which maintains a laboratory colony with an annual influx of wild individuals to maintain genetic diversity; we used the eggs to start a short-term colony in a growth chamber in Ithaca, NY (14 h of light (28 μmols/1512 lux): 10 h of dark cycle). This colony provided eggs for each cohort of the experiment in 2023 and was restarted in 2024. Newly hatched first instar larvae from the colony were weighed on a Mettler Toledo XSR204 scale (Columbus, OH, USA) to the microgram before being moved to the field the same day. We randomly placed one larva on the tallest node of a milkweed plant within a smaller 30 × 35 cm mesh cage. Caterpillars were monitored daily and provided with a new plant when needed so they could eat ad libitum throughout the experiment duration. We weighed 7-day-old caterpillars, using a Fuzion Digital Milligram Scale and calculated their growth rate by subtracting it from their first instar weight and dividing by seven (days). We also recorded the days from hatching to pupation (larval duration) and the days to eclosion (pupation duration). In 2023, we started with 10 larvae per cage leading to a final count of 110 caterpillars per light treatment. In 2024, we started with 30 caterpillars

(15 per light treatment) and concluded the experiment with 14 butterflies.

Butterfly collection and processing

We recorded the eclosion dates of adults and left them in the field for 24 h to allow their wings to fully dry (Freedman et al., 2020). The following day, we recorded their sex and tested each individual for *Ophryocystis elektroschirrha* (OE), a protozoan parasite, by placing tape to their abdomen and looking for spores underneath a microscope (Altizer & Oberhauser, 1999). We then placed the butterflies in a labeled glassine envelope inside a cooler with freezer packs and transported them back to the laboratory, where a wet mass was recorded for each individual ($n = 127$ butterflies). The butterflies were placed in a −80 freezer for 24 h, freeze-dried, and weighed again to get a dry mass ($n = 62$ butterflies). Dry mass measurements were only possible for butterflies that eclosed in cohorts 1 and 2 in 2023, since the individuals in Cohort 3 in 2023 and Cohort 4 in 2024 were dissected to confirm reproductive diapause. However, there was only one individual per host plant that was not in reproductive diapause; accordingly, diapause was not used as a metric of performance.

Wing imaging and processing

We removed the right forewing of each individual and placed it next to a millimeter ruler inside a Depthlan 25 cm light box. We photographed each wing with a Nikon DSLR (D 5100 series) camera set to a height of 17 cm, a speed of 1/25, an aperture of F16, and an ISO of 100. To measure forewing length, we calibrated each image in ImageJ (Schneider et al., 2012) by outlining a millimeter from the ruler before measuring the length of the wing (as shown in Appendix S1: Figure S3). We calculated the surface area of the right forewing and hindwing in square millimeters using ImageJ (Schneider et al., 2012) and multiplied each wing by two to get a predicted measurement of the total wing area (in square millimeters). We divided each butterfly's wet mass by their total wing area to get a measurement of their wing loading (in milligrams per square millimeter) (Davis & Holden, 2015; Soule et al., 2020; Appendix S1: Figure S3).

Statistical analysis

We fit linear mixed-effects models (LME) using package lme4 (Bates et al., 2003) in RStudio (version 2023.09.1+494). We initially included all potential interactions between treatment, cohort, sex, host plant species, and initial mass, then removed any interaction that was not significant at the 0.05 level to arrive at a minimal adequate model. We also included a random factor that accounted for the nonindependence among individuals in the same cage for each cohort. A Type II analysis of variance was run on each model using the function anova (marginal) within the stats package to calculate the marginal sums of squares. Additionally, we used the package car (Fox et al., 2007) to conduct a Type III analysis of variance on the performance metrics where there was a significant interaction (only ran on wing surface area). Next, we ran Tukey's post hoc pairwise comparisons on the model to identify which treatment groups significantly differed from one another. We then used the package emmeans (Lenth, 2017) to predict the estimated marginal means from the model. These emmean predictions were represented in the figures on top of the raw data points. *Survival*: We used the package survival (Therneau, 2001) to fit Kaplan–Meier survival models to assess whether the treatment groups had any effect on survival throughout development. *Covariance in mass measurements*: We then performed linear regression (using the function lm as a part of the Base R package) to examine the effects of light treatment on adult dry mass, controlling for variation in adult wet mass. The full model included fixed effects of treatment, sex, species, and cohort, as well as the interaction between treatment and adult wet mass to assess whether the relationship between fresh and dry mass differed across treatment conditions.

Path analysis

To assess the sequential relationships among developmental and morphological traits, we constructed a path analysis using structural equation modeling (SEM) through the lavaan package (Rosseel, 2012). We assembled the path to test each direct and indirect effect of ALAN and the other categorical variables on each of the monarchs' traits according to prior knowledge about their life history and plasticity under varying biotic (Agrawal et al., 2021) and abiotic conditions (Nail et al., 2015). For example, we aimed to pick apart whether ALAN had a direct influence on body size or if the observed change in size occurred indirectly through ALAN mediated changes in growth (Appendix S1: Figure S4). Through testing each of these different paths, we could critically evaluate the relationships between life history traits (growth rate, developmental timing, and final body size—measured by fresh body mass and wing

surface area) as well as how their relationships are influenced by host plant, seasonality, sex, as well as the addition of ALAN (Appendix S1: Figure S4).

We grouped together cohorts 1 and 2 to represent early season monarchs and cohorts 3 and 4 as late season butterflies that were confirmed to be in reproductive diapause after being exposed to shorter photoperiods and colder nighttime temperatures. This seasonal grouping allowed seasonality to be dummy-coded in the path analysis (Appendix S1: Table S7). The fit of the model was then assessed using the comparative fit index (CFI = 1.00), the Tucker–Lewis Index (TLI = 1.069) and root mean square error of approximation (RMSEA < 0.08; Appendix S1: Table S8).

RESULTS

ALAN impacts growth and development

Larval exposure to ALAN increased growth rate of early instar caterpillars by 16% ($F_{(1,\ 18)} = 4.292$, $p = 0.053$; Figure 1A; Appendix S1: Table S2A). Caterpillars spent approximately 3% less time in the larval stage ($F_{(1,\ 22)} = 2.509$, $p = 0.128$; Figure 1B; Appendix S1: Table S2B) and nearly 5% longer as pupa under ALAN ($F_{(1,\ 22)} = 4.755$, $p = 0.040$), leading to their total development time being unaffected by light treatment. Nonetheless, monarchs grew to be >7% heavier under ALAN ($F_{(1,\ 24)} = 7.958$, $p = 0.010$; Figure 2A; Appendix S1: Table S2C). However, other metrics of butterfly performance, including dry mass ($F_{(1,\ 11)} = 1.109$, $p = 0.315$; Figure 3A; Appendix S1: Table S2E), forewing length ($F_{(1,\ 22)} = 2.628$, $p = 0.119$), and wing loading ($F_{(1,\ 23)} = 1.744$, $p = 0.200$; Figure 3B,C; Appendix S1: Table S4D), were unaffected by ALAN. We found a positive correlation between fresh and dry mass (estimate = 0.247 ± 0.043, $t = 5.678$, $p < 0.001$; Figure 3A; Appendix S1: Table S6) under control light, and this relationship was attenuated (weaker slope) in the presence of ALAN: butterflies accumulated more fresh mass per unit dry mass under ALAN compared to the controls (estimate = -0.135 ± 0.047, $t = -2.842$, $p = 0.006$; Figure 3A; Appendix S1: Table S6).

Growing season influences performance

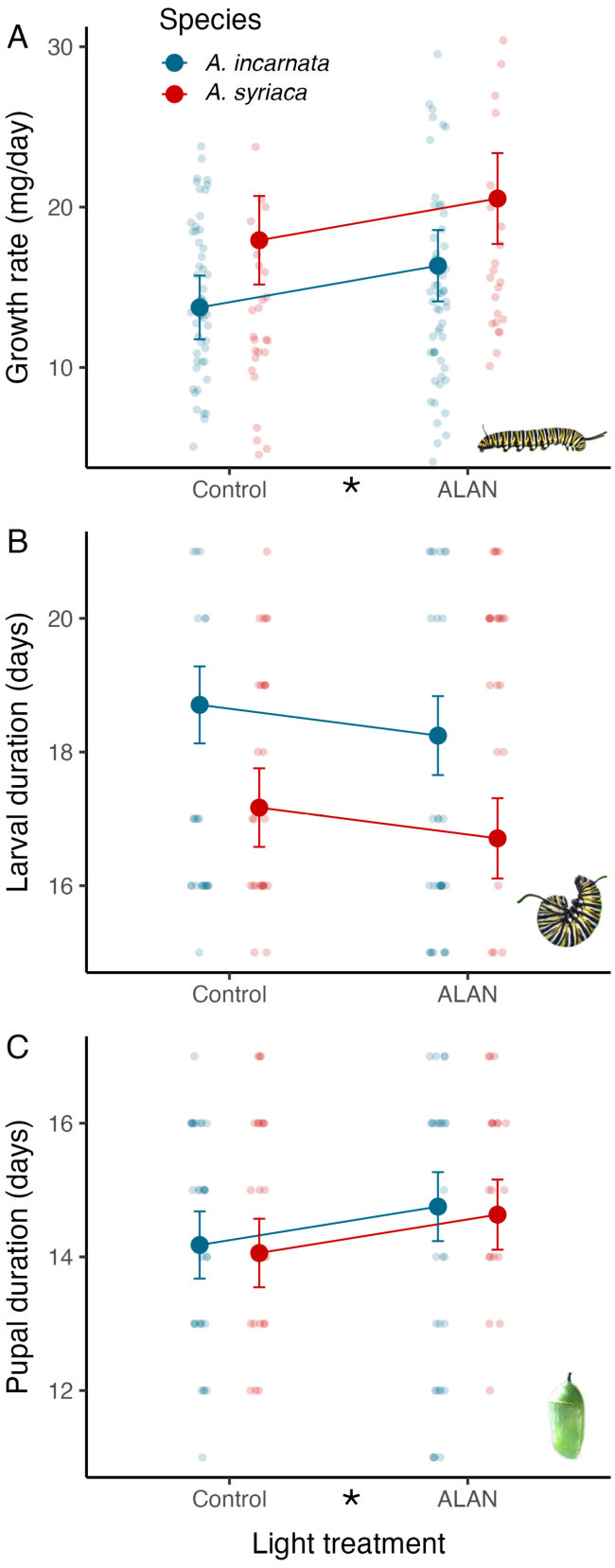
The life history of the two early summer generation cohorts (1: June–2: July) drastically differed from the two late summer cohorts (4: August–3: September). Caterpillars that eclosed in September (Cohort 3) grew 34% less per day ($t_{18} = -3.237$, $p = 0.004$) and developed 36% slower as larva ($t_{22} = 13.105$, $p < 0.001$) than the caterpillars in June (Cohort 1). Additionally, the late season pupae in August and September remained in their chrysalids approximately 11 days longer than those in June (32%), (Cohort 3: $t_{22} = 9.617$, $p < 0.001$, Cohort 4: $t_{22} = 6.030$, $p < 0.001$). The seasonal decline in temperature and photoperiod throughout the summer correlated with the reduction of body mass among butterflies in July ($t_{24} = -4.257$, $p < 0.001$), August ($t_{24} = -6.057$, $p < 0.001$), and September ($t_{24} = -11.350$, $p < 0.001$). By the start of autumn, monarchs that eclosed in September weighed 44% less than those reared in June (Cohort 1) ($t_{24} = -11.350$, $p < 0.001$; Figure 2A; Appendix S1: Table S3). This dramatic loss in mass across the summer generations contributed to a 30% decline in wing loading (in milligrams per square millimeter) among late season butterflies (August and September) compared to the early season individuals in July (Cohort 3: $t_{23} = -7.347$, $p < 0.001$, Cohort 4: $t_{23} = -5.591$, $p < 0.001$; Figure 4C; Appendix S1: Table S5).

Interactive effects of host plant on ALAN sensitivity

Host plant shaped larval growth, development time, and wing morphology under both light treatments (Figures 1–3B; Appendix S1: Tables S2 and S4). Caterpillars reared on *A. syriaca* grew 26% more ($F_{(1,\ 84)} = 8.725$, $p = 0.004$; Figure 1A; Appendix S1: Table S2A) and developed 10% faster ($F_{(1,\ 79)} = 22.029$, $p < 0.001$; Figure 1B; Appendix S1: Table S2B) than caterpillars on *A. incarnata*. Host plant also affected wing shape; an *A. syriaca* diet increased forewing length by 4% ($F_{(1,\ 83)} = 8.725$, $p = 0.004$; Figure 3B; Appendix S1: Table S4A), while the total wing surface area remained the same between host plants ($F_{(1,\ 75)} = 2.519$, $p = 0.117$). Despite these plant mediated differences in growth, development, and wing morphology, host plant did not affect butterfly fresh mass ($F_{(1,\ 91)} = 1.058$, $p = 0.307$; Figure 2A; Appendix S1: Table S2D) or dry mass ($F_{(1,\ 43)} = 0.110$, $p = 0.742$; Appendix S1: Table S3E). Interestingly, host plant mediated the effect of ALAN on wing area—*A. syriaca* monarch wings were 7% larger under ALAN compared to the control while *A. incarnata* wing size was not affected (host plant × ALAN interaction, $F_{(1,75)} = 4.635$, $p = 0.035$; Figure 2B; Appendix S1: Table S4C).

Path analysis on effects of ALAN on growth and development

As a means to link the impacts of ALAN over the monarch's life-cycle, we conducted a path analysis. This



allowed us to identify the most sensitive life stages and determine whether effects at those stages propagate through the trajectory of their development. Additionally, because host plants, seasonal cohort, and sex each influenced monarch development, an integrated path analysis allowed us to simultaneously measure the direct and indirect influences of each abiotic and biotic variable on their performance. The presence of light at night had as much of a positive effect on larval growth ($\beta' = 0.221$, $p = 0.028$, Figure 4; Appendix S1: Table S6) as the difference in growth on *A. incarnata* versus *A. syriaca* ($\beta' = 0.204$, $p = 0.05$, Figure 4). Larval duration was minimally affected by ALAN ($\beta' = -0.072$, $p = 0.154$), but directly negatively affected by growth rate ($\beta' = -0.17$, $p = 0.001$) and host plant ($\beta' = -0.185$, $p < 0.001$), signifying that a diet of *A. syriaca* decreased larval duration through increased growth. Comparatively, slower growth in late season ($\beta' = -0.289$, $p = 0.006$) resulted in prolonged time spent as a caterpillar ($\beta' = 0.853$, $p < 0.001$) as well as pupa ($\beta' = 1.201$, $p < 0.001$), leading to smaller late season butterflies ($\beta' = -0.481$, $p = 0.006$; Figure 4). Sexual dimorphism emerged in the pupal stage with males spending longer in chrysalids than females ($\beta' = 0.155$, $p = 0.01$), which was linked to males having larger fresh mass than females ($\beta' = 0.296$, $p < 0.001$). Overall, butterflies also grew to be heavier under ALAN ($\beta' = 0.137$, $p = 0.02$). While ALAN did not have a direct effect on wing area ($\beta' = 0.07$, $p = 0.443$), it did indirectly increase butterfly wing size through the significant positive effect on fresh mass.

DISCUSSION

Our results reveal that ALAN increased the growth (Figure 1A), pupal duration (Figure 1C), and fresh mass of monarchs (Figure 2A). Nonetheless, this did not

FIGURE 1 (A) Growth rate, (B) larval duration, and (C) pupal duration of monarch caterpillars between light treatments. Host plants are represented by colors, with *Asclepias incarnata* in blue and *Asclepias syriaca* in red. Shown are the predicted means and 95% CI from linear mixed models over the raw data. The asterisks on the *x*-axis indicate significance of light treatment on the growth rate ($p = 0.038$) and pupal duration ($p = 0.029$) (Appendix S1: Table S2). Photo credits: A. A. Agrawal (A and B) and Hannah Gurholt (C).

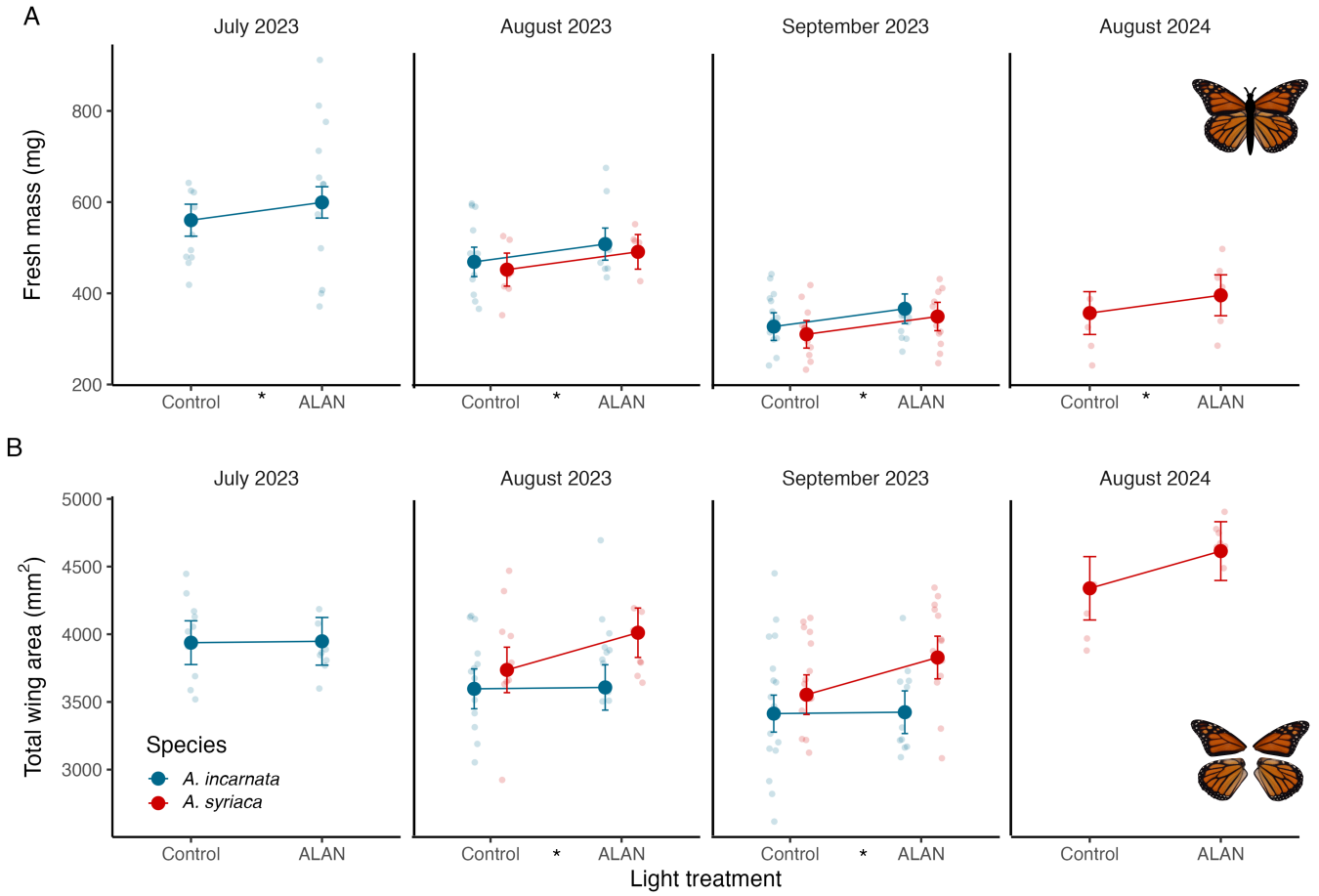


FIGURE 2 (A) Fresh mass (in milligrams) and (B) total wing area (in square millimeters) of adult monarchs between light treatments. Host plants are represented by colors, *Asclepias incarnata* in blue and *Asclepias syriaca* in red. Shown are the predicted means and 95% CI from linear mixed models with the raw data points. The asterisks indicate significance of light treatment on the adult wet mass ($p = 0.002$; Appendix S1: Table S2) and the interaction between species and light treatment on the total wing area ($p = 0.031$; Appendix S1: Table S4). Butterfly images by Hannah Gurholt.

translate to an effect on dry mass, raising the question of whether caterpillars that developed under ALAN attained more water as they grow faster. The increase in growth and mass is likely due to caterpillar feeding times being extended into the night under ALAN (Haynes et al., 2023; Macgregor et al., 2015; Owens et al., 2020; Owens & Lewis, 2018; Wilson et al., 2021). For example, in the only other study of ALAN on monarch performance, Haynes et al. (2023) found that caterpillars spent twice as much time feeding on milkweed when under light at night. Increased consumption through elongated activity times under ALAN has been found in other diurnal phytophagous insects (Sanders et al., 2021), signifying the physiological sensitivity of diurnal herbivores. Larger size often correlates with higher fecundity (in resident butterflies) and greater flight success (in migratory butterflies), suggesting that ALAN may enhance the performance of migratory and nonmigratory monarchs (Blanckenhorn, 2000; Nylin & Gotthard, 1998). Our results contrast with previous findings showing the detrimental effects of light on the life history and fitness of other insects (Manfrin et al., 2025; McLay et al., 2017; Willmott et al., 2018). Nonetheless, we are cautious with this conclusion, as the trajectory induced by light at night may have caused other changes, for example in body composition, not examined in this study.

As another metric of performance, we measured the effect of ALAN on wing morphology, including forewing length, total wing surface area, and wing loading—all critical for the dispersal of resident butterflies in the summer and the migratory success in the fall (Johnson et al., 2014; Soule et al., 2020). However, larval exposure to ALAN appeared to have minimal effects on forewing length on either host plant (Figure 3B). ALAN also did not influence the total surface area of butterflies reared on *A. incarnata* (Figure 2B), but butterflies that fed on *A. syriaca* developed significantly larger wings under ALAN, likely increasing their flight performance

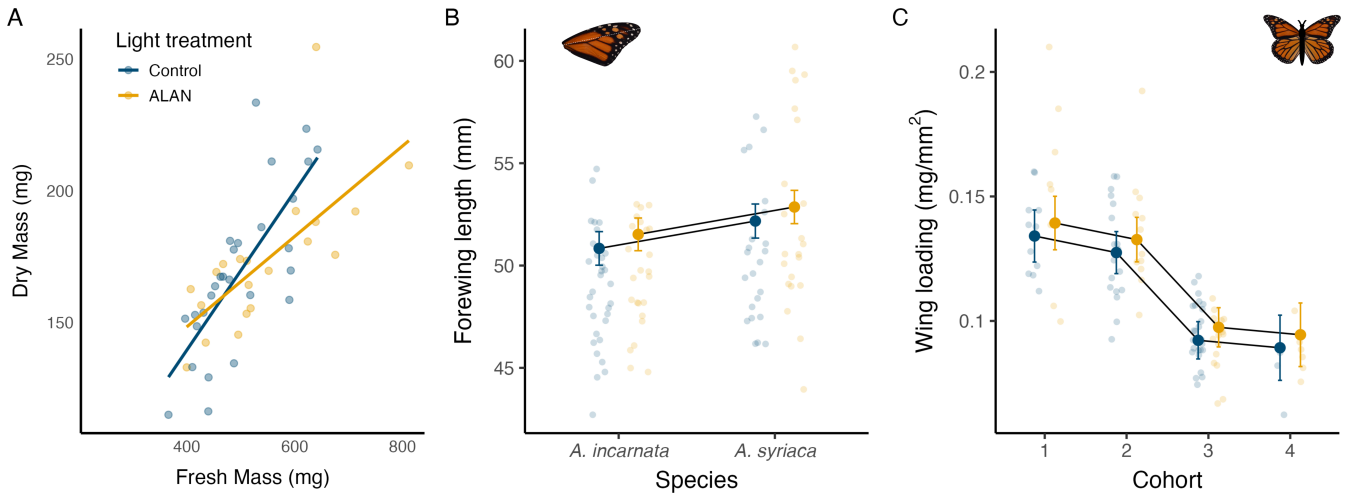


FIGURE 3 (A) Correlation between adult fresh and dry mass, (B) forewing length (in millimeters), and (C) wing loading (in milligrams per square millimeter) ability of monarchs between light treatments. Light treatment is represented by colors, control in dark blue and artificial light at night (ALAN) in yellow. The raw data points are plotted in (A) along with the slope for each light treatment (Appendix S1: Table S6). Shown are the predicted means and 95% CI from linear mixed models for (B) and (C) with the raw data points (Appendix S1: Table S4). Wing and butterfly by Hannah Gurholt.

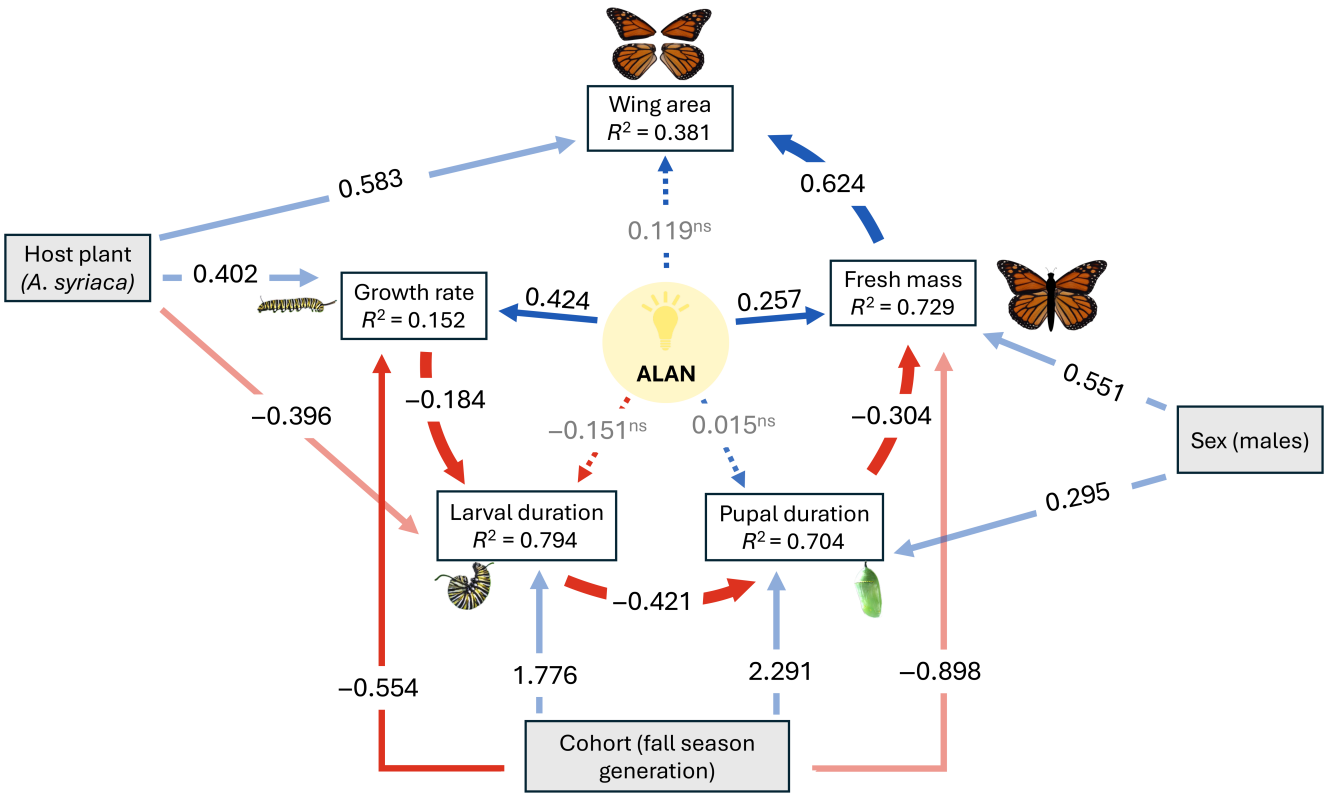


FIGURE 4 Path analysis of the predictors of development and life history traits of monarchs (refer to Appendix S1: Figure S4 for the conceptual framework of the path analysis). Filled arrows represent the significant paths ($p < 0.05$) with red being negative and blue positive. Significant standardized coefficients are represented by black text and fully colored in lines. Comparatively, dotted lines with gray text represent nonsignificant standardized coefficients ($p > 0.05$). There were no significant indirect effects of treatment on any of the life history traits, therefore only the direct relationships are represented in the figure. Refer to Appendix S1: Table S8 for significance tests, including the fit indices (CIT = 1, TLI = 1.069, and RMSEA < 0.008). Caterpillar and chrysalis by A. A. Agrawal. Butterfly images by Hannah Gurholt. Figure created by Hannah Gurholt using lightbulb and arrow icons from Keynote.

(Altizer & Davis, 2009; Flockhart, 2017). This suggests that while host plant did not influence the sensitivity of monarchs to ALAN on measures taken during larval or pupal stages, it did modify physiology that manifested after adult eclosion (Figure 2B). Our findings are supported by other studies that found host plant mediates how monarchs respond to elevated temperatures (Faldyn et al., 2018) and pesticides (Prouty et al., 2021).

One strength of our study was the inclusion of multiple generations of monarchs across 2 years in the field experiments over the full course of development. Through raising caterpillars from June–September in the field, we investigated how ALAN can affect the monarchs during the summer breeding season versus their migratory generation. A contrast between the July (1) and August (2) cohorts in 2023 with the September (3) 2023 and August (4) 2024 cohorts showed the latter two cohorts were all confirmed to be in reproductive diapause, indicating that they were likely initiating migration (although not all monarchs in diapause are migratory). Individuals in diapause were roughly 44% lighter than the butterflies in the first summer generation (Figure 2A), and this effect may be due to both the direct effects of changing seasonal conditions and the induction of diapause and migration. Subsequently, the wing loading of these diapausing monarchs was roughly 30% less than the first summer generation (Figure 3C); this result conflicts with previous findings that diapausing monarchs are typically larger than those from earlier reproductively active generations (Altizer & Davis, 2009; Flockhart, 2017), and may have been influenced by the specific climatic conditions experienced by caterpillars in our field. However, the addition of ALAN may benefit breeding and diapausing monarchs by increasing their fresh mass (Figure 2A). For breeding butterflies, ALAN can increase their dispersal ability for finding mates and nectar rich habitats. Similarly, the size increase under ALAN may provide more energy reserves for better flight success among diapausing butterflies. Overall, our findings suggest (1) the influential role of seasonality on development, and (2) the consistent effect of ALAN across all four summer and early fall generations, signifying the uniform effect of light pollution on the development.

In 2020, the U.S. Fish and Wildlife Service determined that protection of the monarch butterfly under the Endangered Species Act was "warranted but precluded by higher-priority actions," and again proposed listing it as threatened in 2024 (U.S. Fish and Wildlife Service, 2020, 2024). This finding stressed the importance of identifying anthropogenic threats to the monarch and other declining species. In response to conservation concerns, there have been large-scale restoration projects geared towards expanding milkweed habitat along their migratory route (Thogmartin et al., 2017), including metropolitan areas (Johnston et al., 2019) where ALAN is prevalent (Operti et al., 2018; Pothukuchi, 2021). However, the extent to which ALAN exposure affects caterpillar development and adult performance in these light-polluted habitats remains unknown. Utilizing 2 years of field experiments on four generations of monarchs, we gained an understanding of how ALAN influences the growth, development, and performance of this flagship species. Still, work on diapause, migratory orientation and flight, and body composition are needed to understand the full effects of ALAN.

To our knowledge, ours is the first study to (1) elucidate the direct relationships between growth, development, and performance across multiple generations of the monarch butterfly and (2) illustrate how the anthropogenic stressor of ALAN influences each trait individually, as well as how they interact with one another. Together these results show that while the spread of ALAN is concerning for wildlife generally and migratory species in particular (Parlin et al., 2022), ALAN may have a positive effect on the development and performance of this diurnal, phytophagous insect. For the monarch, these findings indicate that expanding roadside restoration projects near sources of ALAN may not harm their development and performance. Nonetheless, as with all species, impacts of higher trophic levels and other forms of anthropogenic stress, such as the blend of noise pollution and heat in the urban matrix (Willems et al., 2022; Wilson et al., 2021), may conspire with the effects observed here. Indeed, our strongest finding is that monarch caterpillars are set off on divergent growth trajectories under ALAN, and the ecophysiological basis and ultimate consequences of this shift are yet to be uncovered.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Gurholt et al., 2026) are available in Cornell University Library eCommons at https://doi.org/10.7298/PARD-TT61.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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