PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research

**Cite this article:** Deitsch JF, Kaiser SA. 2023 Artificial light at night increases top-down pressure on caterpillars: experimental evidence from a light-naive forest. *Proc. R. Soc. B* **290**: 20230153.
https://doi.org/10.1098/rspb.2023.0153

Received: 11 October 2022
Accepted: 13 February 2023

**Subject Category:**
Ecology

**Subject Areas:**
ecology, behaviour

**Keywords:**
artificial light at night, predation, sensory pollution, community composition, caterpillars, LED lighting

**Author for correspondence:**
Sara A. Kaiser
e-mail: sak275@cornell.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.6440235.

THE ROYAL SOCIETY PUBLISHING



# Artificial light at night increases top-down pressure on caterpillars: experimental evidence from a light-naive forest

John F. Deitsch[1,2] and Sara A. Kaiser[3]

[1]Department of Entomology, [2]Department of Biological Sciences, and [3]Center for Biodiversity Sciences, Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850, USA

SAK, 0000-0002-6464-3238

Artificial light at night (ALAN) is a globally widespread and expanding form of anthropogenic change that impacts arthropod biodiversity. ALAN alters interspecific interactions between arthropods, including predation and parasitism. Despite their ecological importance as prey and hosts, the impact of ALAN on larval arthropod stages, such as caterpillars, is poorly understood. We examined the hypothesis that ALAN increases top-down pressure on caterpillars from arthropod predators and parasitoids. We experimentally illuminated study plots with moderate levels (10–15 lux) of LED lighting at light-naive Hubbard Brook Experimental Forest, New Hampshire. We measured and compared between experimental and control plots: (i) predation on clay caterpillars, and (ii) abundance of arthropod predators and parasitoids. We found that predation rates on clay caterpillars and abundance of arthropod predators and parasitoids were significantly higher on ALAN treatment plots relative to control plots. These results suggest that moderate levels of ALAN increase top-down pressure on caterpillars. We did not test mechanisms, but sampling data indicates that increased abundance of predators near lights may play a role. This study highlights the importance of examining the effects of ALAN on both adult and larval life stages and suggests potential consequences of ALAN on arthropod populations and communities.

## 1. Introduction

Artificial light at night (ALAN) is increasingly being recognized as a threat to insect biodiversity, impacting a variety of insect taxa and behaviours [1–3]. Globally, ALAN is increasing in both extent of areas illuminated and radiance (brightness) levels [4] and has been identified as a potential driver of insect declines [5,6]. ALAN alters natural cycles in nocturnal light levels that are important behavioural and physiological cues for many arthropods [3]. ALAN affects many aspects of insect life history—including reproduction [7,8], development [9] and navigation [1,10]. Species interactions are impacted by nocturnal light pollution as well, including pollination [11,12], predation [13–15] and parasitism [16,17]. These and other impacts result in changes to community composition and structure [18].

Despite an increase in studies examining the impacts of ALAN on adult life stages of insects, particularly moths, our understanding of how insect populations respond to ALAN remains incomplete [19]. Few studies have investigated the impacts of ALAN on earlier life stages of insects, such as larvae (caterpillars) and pupae [20]. Consequently, the effects of ALAN on caterpillar development, predation and parasitism, and behaviour remain poorly understood. This is a critical knowledge gap because: (i) caterpillars are important for terrestrial ecosystems, including as prey for predators and hosts for parasitoids, (ii) many caterpillars feed at night to minimize predation and parasitism risk [21,22], and (iii) conditions during larval development affect adult fitness [9]. Additionally, evidence suggests that caterpillar abundance can be reduced around sources of ALAN [23].

ALAN has been found to alter arthropod communities through top-down effects mediated by predators and parasitoids, but this has yet to be demonstrated in caterpillars. ALAN is hypothesized to impact top-down pressure on arthropods via multiple mechanisms [20]. The abundance of arthropod predators and scavengers is often elevated near artificial light sources—attracted by the presence of immobilized prey or via positive phototaxis [15,24,25]. Many parasitoid wasps also display positive phototaxis, which could lead to locally higher densities of parasitoids around light sources, although parasitoids have received less attention than predators [19]. Additionally, diurnal predators and parasitoids can exploit the 'nightlight' niche provided by ALAN and forage nocturnally. Temporal niche expansion owing to ALAN has been observed in parasitoid wasps (Ichneumonidae) [26], jumping spiders (Salticidae) [27] and wasps (Vespidae) [28]. Top-down pressure on caterpillars from predators and parasitoids has rarely been explored within the context of ALAN [19]. One previous study found that immobilized moth larvae did not suffer increased predation under streetlights [29]. However, ALAN has been shown to increase top-down pressure on other insect taxa. For example, top-down control of aphids by predatory ladybeetles (Coccinellidae) [30] and parasitoids wasps (Braconidae) [26,31] was higher under ALAN, and nocturnal predation of immobilized fruit flies was higher under ALAN [15]. Top-down pressure on caterpillars could also be affected indirectly by ALAN-induced alterations of host-plant quality. Reduction in host-plant quality could lengthen larval development, increasing exposure to predators and parasitoids [32]. Increased top-down pressure under ALAN observed in other insect taxa combined with recent evidence of decreased caterpillar abundance near light sources suggest that ALAN may facilitate increased predation and parasitism of caterpillars.

In this study, we experimentally examined the hypothesis that ALAN influences top-down pressure on caterpillars from arthropod predators and parasitoids at the light-naive Hubbard Brook Experimental Forest, New Hampshire. To assess the effects of ALAN on top-down pressure, we measured predation rates on clay caterpillars and compared predation rates between experimentally illuminated (treatment) plots and naturally illuminated (control) plots. Concurrently, we sampled insects on treatment and control plots to monitor the response of the arthropod community to the experimental light treatment in a light-naïve northern hardwood forest. On experimental plots relative to control plots, we predicted that: (i) predation rates on clay caterpillars would be higher, and (ii) arthropod predator and parasitoid abundance would be higher. We further predicted that the effect of ALAN on predation rates and the arthropod community would increase over the study period owing to the accumulation of predators and parasitoids near light sources over time.

## 2. Methods

### (a) Study area

We conducted this experiment at the Hubbard Brook Experimental Forest (Hubbard Brook), New Hampshire, USA (43.56° N, 71.45° W). The study area is located within 3160 ha of mature mixed-hardwood forest with an overstory dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*) [33,34]. The understory is primarily composed of hobblebush (*Vibernum lantanoides*) and saplings of striped maple (*Acer pensylvanicum*) and major canopy species. No permanent sources of light pollution are present in the forest interior at Hubbard Brook, maximizing the difference in night-time illumination between experimental and control plots [19]. Several hundred species of Lepidoptera have been identified at Hubbard Brook, as well as a diverse community of arthropod predators and parasitoids [35]. Long-term insect sampling has shown no consistent seasonal peak in biomass across years for Lepidopteran larvae or flying insects [36].

### (b) Experimental design

To test the impacts of ALAN on caterpillar predation rates and the arthropod community, we established eight study plots in a paired design ($n = 4$ pairs), with each experimental plot paired to a control plot. Owing to steep topography of the study area, plots were separated into two blocks of four plots (figure 1*a*). Paired experimental and control plots were separated by 50 m, paired plots within a block by 100 m and blocks of four plots by 350 m. To minimize variation in arthropod communities among plots, we chose plots with similar vegetation composition and canopy structure (i.e. similar natural light levels). At the centre of each plot, we established a Malaise trap. Light sources on experimental plots were placed 8–10 m from the Malaise trap. We placed pan traps midway between the Malaise trap and the light source on experimental plots and 4–5 m from the Malaise trap on control plots (figure 1*c*). The road parallel to the four plot pairs (figure 1*a*) is non-paved and has no permanent light sources. Edge and interior plots were 25 m and 75 m from the road, respectively.

Each experimental plot was illuminated by one unidirectional 6 W solar-powered light-emitting diodes (LED) flood light (5000 K CCT, < 600 lumens, LED Lighting Solutions). Lights were affixed to tree trunks 2–3 m above the ground and directed downwards at roughly 45° towards the centre of the plot (i.e. the Malaise trap). Lights were not powerful enough to result in spillover illumination on control plots (figure 1*b*). We chose LED because the outdoor lighting market is trending towards more energy-efficient broad-spectrum LED lights [4]. Additionally, studies have suggested that LEDs could have a greater impact on ecosystems than narrow-spectrum lighting such as high-pressure sodium [37].

Experimental plots were illuminated from 7 June to 29 July 2021 (7.5 weeks). We confirmed that lights were functional after sunset four times throughout the study period (16 June, 23 June, 22 July and 28 July). We sampled arthropods from 31 May to 30 July (8.5 weeks) with Malaise traps and from 8 June to 27 July (7 weeks) with pan traps. We deployed plasticine clay caterpillar models (clay caterpillars) during four sampling periods over the study period (12–15 June, 25–28 June, 10–13 July and 24–27 July). The first and third sampling periods occurred during the new moon phase and the second and fourth sampling periods occurred during the full moon phase. Temperature and light intensity (lux) measurements were recorded every 15 min from 31 May to 30 July (8.5 weeks) using HOBO Temperature/Light Data Loggers (UA-002-08). Data loggers were located on five of the eight plots (three experimental plots and two control plots). We placed data loggers such that each block had one pair of experimental/control plots both with data loggers. We obtained daily temperature and rainfall data from a U.S. Forest Service weather station (approx. 500 m above sea level, located 0.2 km from the study area).

### (c) Caterpillar predation experiment

We estimated caterpillar predation rates using clay caterpillars (figure 2*a–e*), which is a technique effectively used to measure and compare caterpillar predation rates in a wide variety of habitats [38–40], including a previous study at Hubbard Brook [41]. We made caterpillar models with non-hardening green modelling clay (Sargent Art) using a clay extruder (Walnut Hollow)

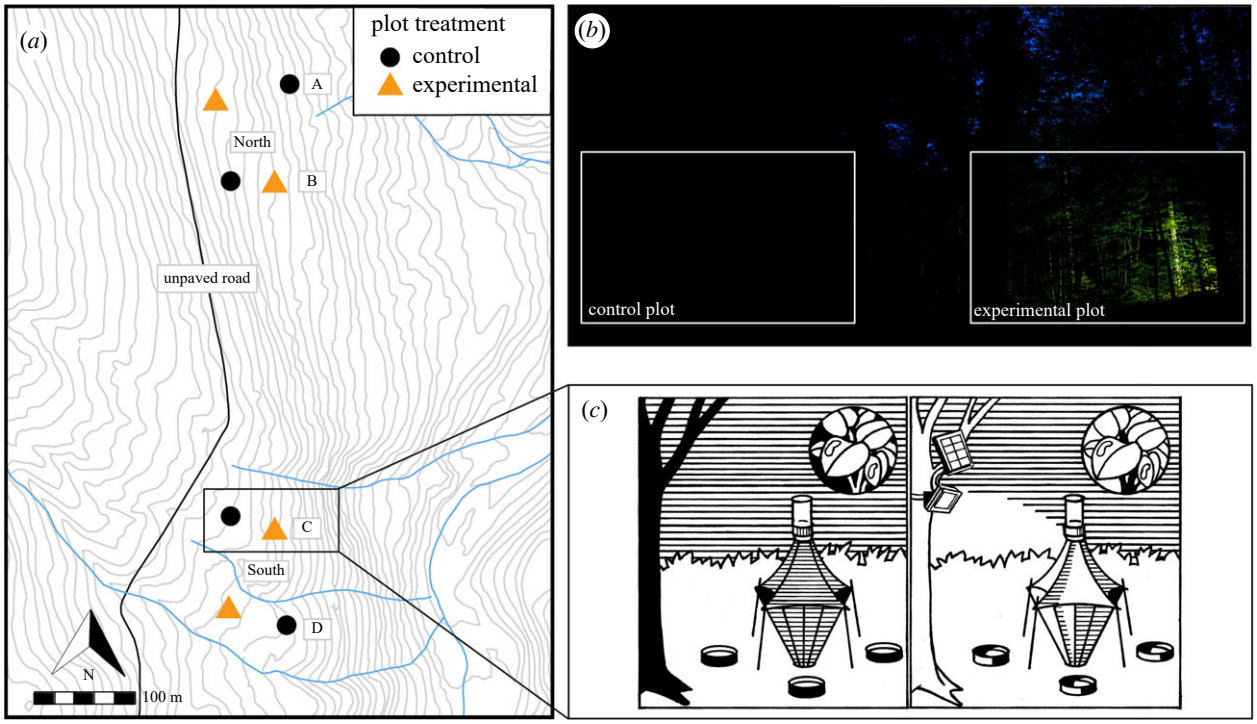


**Figure 1.** (*a*) Contour map of the study area at the Hubbard Brook Experimental Forest, New Hampshire, USA. Eight study plots (four experimental, four control) were established in a paired design on the east side of the U.S. Forest Service Road. Plots were split into two blocks of four plots (North, South) owing to steep topography. Distances between plots are provided in the electronic supplementary material, table S8. (*b*) Photo showing the difference in night-time illumination between experimental and control plots. Photos depicting habitat similarities across plots are provided in the electronic supplementary material, figure S4. (*c*) Schematic of the experimental design of the plasticine clay caterpillar experiment and concurrent arthropod sampling on experimental and control plots (illustration by David Kaiser).

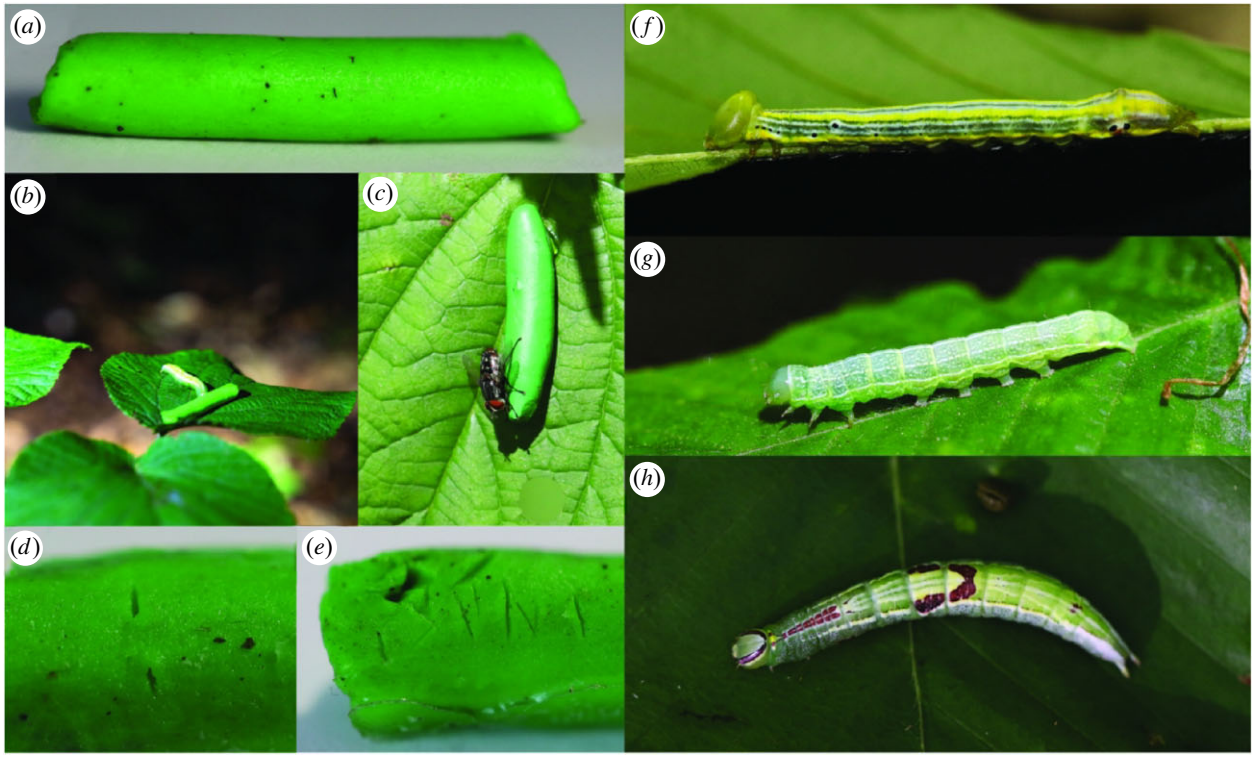


**Figure 2.** Images of the plasticine clay caterpillar model predation experiment at the Hubbard Brook Experimental Forest, New Hampshire, USA: (*a*) plasticine clay caterpillar model before deployment into the field, (*b*) clay caterpillar model beside live Heterocampa (Notodontidae) caterpillar, (*c*) clay caterpillar model with Tachinid fly, (*d*,*e*) examples of marks left by arthropods (examples of non-arthropod marks in the electronic supplementary material, figure S5), and (*f*–*h*) live caterpillars observed in the study area and used as models for plasticine clay caterpillars (*f*: Notodontidae, *g*: Noctuidae, *h*: Notodontidae).

to reduce variability in size and shape among models. Caterpillar models were 30 ± 3 mm in length and 4.5 ± 0.25 mm in diameter (figure 2*a*). We chose the colour and size to mimic Noctuidae (owlet moths) and Notodontidae (prominent moths) caterpillars commonly sampled in the understory at Hubbard Brook (figure 2*f*–*g*). We deployed 17 ± 2 caterpillar models on each

plot during each of four sampling periods across the study period. We glued caterpillar models to hobblebush and striped maple leaves 0.1–1 m above the ground. Caterpillar models on experimental plots were approximately 5 m from the light source. We used a paper hole puncher to make two holes in each model-bearing leaf to roughly imitate natural patterns of herbivory and to release volatile organic compounds that predators and parasitoids use as cues to find prey [40]. We handled caterpillar models by their ends during placement and retrieval to minimize accidental markings. We collected the caterpillar models from the field after 72 h and assessed models under a dissecting microscope to identify and record predation marks. Marks were coarsely classified (predatory arthropod, parasitoid arthropod, bird, mammal, or unknown/other); finer taxonomic classification is not reliable [42]. We recorded a small number of marks that we classified as 'likely parasitoid arthropod', but because clay caterpillars do not reliably measure response from parasitoids, we did not analyse these data to test the effect of ALAN on parasitism rates.

## (d) Arthropod sampling

Arthropods were sampled with Malaise traps (2 m, BioQuip) and yellow pan traps (350 ml plastic bowls); two techniques highly effective at capturing Hymenopteran parasitoids [43]. We employed both methods because they sample different arthropod taxa and function via different sampling mechanisms, thus yielding a more comprehensive sample of the arthropod community [43,44]. We collected two to three Malaise samples (open 24–96 h) per week over 8.5 weeks on each plot from 31 May to 30 July ($n = 21$ sampling periods). We collected four samples the week before the experimental plots were illuminated on 7 June. Malaise samples were stored in a −80°C freezer until processing. We collected one to two pan trap samples (open 24–144 h) per week over seven weeks on each plot from 8 June to 27 July ($n = 8$ sampling periods). For samples spanning multiple days, sampling day was given as the last day of the sampling period. We placed three yellow pan traps on each plot and filled traps half full (approx. 175 ml) to decrease the likelihood of overflow during rain events. All pan trap specimens were stored in 90% ethanol. We sorted and identified all arthropod specimens sampled in Malaise and pan traps to their Order and identified target taxa (i.e. predators and parasitoids) to Family or Superfamily [45,46].

## (e) Data analysis

### (i) Caterpillar predation experiment

We defined caterpillar predation rate as the proportion of clay caterpillars within a sample that had at least one mark from an arthropod. We calculated predation rate for each plot during each of four sampling periods. We performed a Shapiro–Wilk test on predation rates to confirm normality. We examined spatial variation in caterpillar predation rates by performing one-way ANOVAs on each of the three grouping variables in the plot design (block, pair and proximity to road (edge: 25 m, interior: 75 m)). The road is not a source of ALAN, but we included the road as a possible parameter to control for potential small-scale spatial differences in arthropod communities. Caterpillar predation rate did not vary significantly ($\alpha = 0.05$) between blocks, among pairs, or by proximity to the road; thus, data were pooled within treatments for subsequent analyses.

To test the prediction that predation rates on clay caterpillars would be higher on experimental plots relative to control plots, we constructed a candidate set of linear models with caterpillar predation rate as the response variable. The global model included two fixed effects: treatment (experimental, control) and sampling period [1–4] to account for temporal variation. We checked for autocorrelation among model residuals by constructing an autocorrelation function plot and by conducting a Durbin–Watson test [47]. We performed model selection based on second-order Akaike's information criterion ($AIC_c$) adjusted for small sample sizes [48], using *MuMIn* [49] and ranked candidate models by $\Delta AIC_c$. We averaged statistically indistinguishable candidate models ($\Delta AIC_c < 2$) to obtain coefficient estimates for fixed effects. If one model performed significantly better than all other models ($\Delta AIC_c < 2$), we report coefficient estimates for that candidate model. We summed Akaike weights ($w_i$) across all candidate models to evaluate the relative importance of each fixed effect. If a parameter had a $w_i \geq 0.75$ and a 95% confidence interval (CI) not overlapping zero, we concluded that the parameter had a significant effect on caterpillar predation rate. We examined homogeneity of residuals by plotting model residuals against model-fitted values. We performed a Shapiro–Wilk normality test on model residuals and visually inspected quantile–quantile plots to confirm they were normally distributed [47]. All statistical analyses were conducted in R v. 4.1.1 [50].

We defined the effect of ALAN on caterpillar predation rate as the ratio between caterpillar predation rates on paired experimental and control plots. A ratio greater than or equal to 1 indicates higher caterpillar predation rate on the experimental plot relative to the control plot. We calculated the effect of ALAN on caterpillar predation rate for each plot pair during each sampling period ($n = 16$). We log-transformed ratios and performed a Shapiro–Wilk normality test to confirm normality. To test the prediction that the effect of ALAN on caterpillar predation rate would increase over the study period, we performed a one-way repeated-measures ANOVA (RM-ANOVA) on caterpillar predation rate across sampling periods with plot pair as the identity (ID) variable.

### (ii) Arthropod sampling

We measured daily predator and parasitoid abundance separately from both Malaise and pan trap samples as the 24 h catch rate of predators and parasitoids, respectively. During one pan trap sampling period (28–29 June), elevated rainfall resulted in artificially low estimates of arthropod abundance with several traps overflowing. Therefore, we removed this sampling period from subsequent analyses of abundance in pan traps. We log transformed the four response variables and constructed quantile–quantile plots and histograms to visually examine normality. We examined spatial variation in predator and parasitoid abundance in Malaise and pan trap samples by performing one-way ANOVAs on each of the three grouping variables in the plot design (block, pair, and proximity to road). Statistically significant grouping variables were included in subsequent analyses for that response variable but excluded otherwise. We examined temporal variation in predator and parasitoid abundance in Malaise and pan traps by performing a one-way repeated-measures ANOVA on each response variable across samples with plot as the ID variable.

To test the prediction that arthropod predator and parasitoid abundance would be higher on experimental plots relative to control plots, we constructed a candidate set of generalized least-squares (GLS) models in *nlme* [51] for each of the four response variables described above. We constructed models with a first-order autoregressive correlation structure within each plot to account for serial autocorrelation over time that we detected in initial linear models. Global models included treatment (experimental, control), sampling day and the interaction between treatment and sampling day as fixed effects. To account for environmental variation, the global model also included the 4-day rolling mean temperature (°C) and 4-day rolling mean daily rainfall (mm) as fixed effects. Rolling mean values of temperature and daily rainfall were calculated as right-aligned (including the last day of the sampling period) in *zoo* [52]. To account for significant factors influencing spatial variation in abundance (see ANOVA results), we included block (north, south;

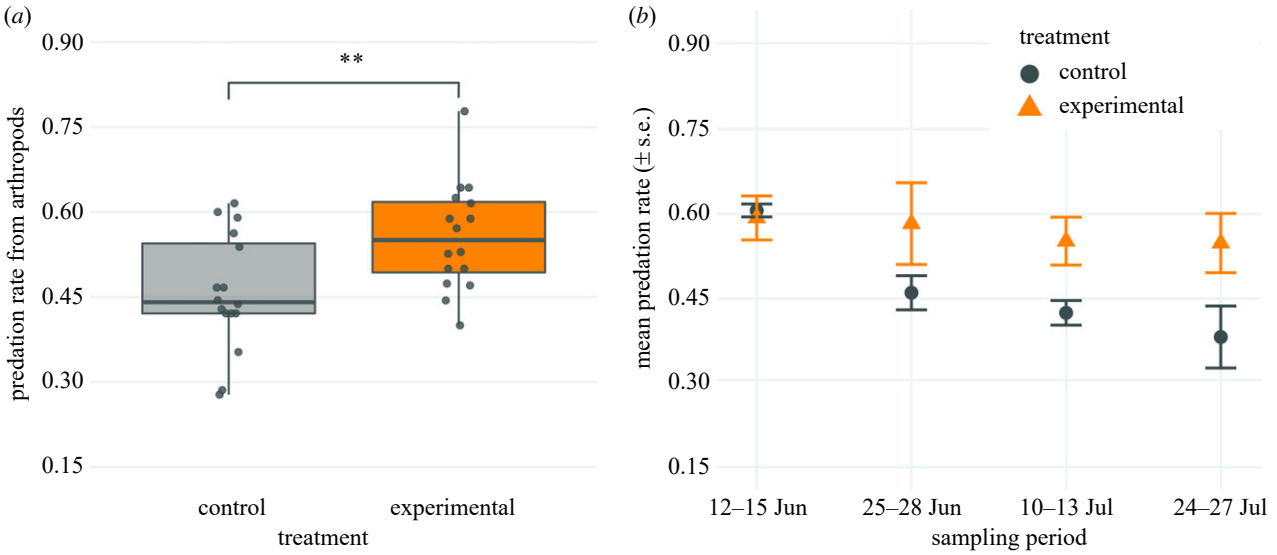


**Figure 3.** (*a*) Mean caterpillar predation rates from arthropod predators on control (45.0 ± 10.0%, $n = 16$) and experimental (56.0 ± 9.0%, $n = 16$) study plots at the Hubbard Brook Experimental Forest, New Hampshire, USA. Points represent individual samples with horizontal jitter. The box and midline represent the 25th, 50th and 75th quartiles; whiskers extend to the most extreme value within interquartile ranges beyond the 25th and 75th percentiles. Asterisks indicate significance at $\alpha < 0.01$ (table 2). (*b*) Mean ± s.e. plasticine clay caterpillar predation rates from arthropod predators on control and experimental plots by sampling period.

**Table 1.** Parameter estimates (± adjusted s.e.), 95% confidence intervals (CI) and summed Akaike weights ($w_i$) for each parameter included in the top-performing candidate linear model experimentally examining the effects of ALAN on predation of plasticine clay caterpillar models by arthropod predators at the Hubbard Brook Experimental Forest, New Hampshire, USA. (The top-performing model was a significantly better fit than other candidate models (electronic supplementary material, table S1). Parameters in italics have CIs that do not include zero.)

| parameter | estimate + s.e. | CI | $w_i$ | $t$ | $p$ | effect[a] |
|---|---|---|---|---|---|---|
| intercept | 0.54 ± 0.04 | 0.45, 0.62 | — | — | — | — |
| *treatment (control)* | 0.09 ± 0.03 | 0.03, 0.16 | 0.95 | 2.90 | *0.007* | +9% predation rate on experimental plots |
| *sampling period* | −0.04 ± 0.01 | −0.07, −0.01 | 0.95 | −2.97 | *0.006* | −4% predation rate per sampling period |

[a]Effect of 1-unit increase in numerical parameter in terms of response variable or the effect of categorical variable level in comparison to reference level.

figure 1*a*) in the global model for predator and parasitoid abundance in pan traps and we included pair (A, B, C, D; figure 1*a*) and proximity to road (edge, interior; figure 1*a*) in the global model for parasitoid abundance in Malaise traps. We scaled numerical effects ($\mu = 0$, s.d. = 1) to account for different levels of magnitude in raw values. We checked for multi-collinearity among predictors as indicated by high variance inflation factors (VIF > 3) and correlation coefficients ($R^2 > 0.7$) [53]. In the pan trap global models, sampling day was correlated with temperature (VIF = 4.3); therefore, we removed temperature from the global models resulting in a maximum VIF = 2.3. We performed model selection as described above (Data analysis: Caterpillar predation experiment). We followed the methods outlined above for taxa of interest sampled in pan and Malaise traps. Taxa-specific results are reported in the electronic supplementary material.

## 3. Results

### (a) Caterpillar predation experiment

Of the 552 clay caterpillars deployed during the study period (4689 caterpillar hours per plot); 31 (5.6%) were lost or damaged in the field and subsequently excluded from analyses. Of the 521 recovered, 249 (47.8%) showed predator marks from arthropods. Mean (±1 s.d.) caterpillar predation rate on control plots was 0.44 ± 0.11 ($n = 16$) and 0.53 ± 0.09 on experimental plots ($n = 16$). The global model in the candidate model set was statistically distinguishable ($\Delta AIC_c > 2$) and accounted for 89% of the total model weight (electronic supplementary material, table S1). The residuals of the global model were normally distributed (Shapiro–Wilk normality test: $W = 0.94$, $p = 0.07$) and were not serially autocorrelated (Durbin Watson test: $D = 2.22$, $p = 0.54$). Treatment and sampling period had a significant effect on caterpillar predation rates (table 1). Caterpillar predation rates were higher on experimental plots than on control plots (figure 3*a*) and declined over the study period on both experimental and control plots (figure 3*b*). The mean (± 1 s.d.) ratio in caterpillar predation rate between paired experimental and control plots was 1.27 ± 0.34 ($n = 16$), indicating caterpillar predation rate was 27% higher on experimental plots than on control plots. The effect of ALAN on caterpillar predation rate appeared to increase over the study period, but this effect was not significant (RM-ANOVA: $F_{1,3} = 2.08$, $p = 0.17$).

### (b) Arthropod sampling

The most-commonly sampled taxa in pan traps were Diaprioidea (Hymenoptera) ($n = 398$), Ichneumonidae (Hymenoptera) ($n = 302$) and Staphylinidae (Coleoptera) ($n = 251$), representing 81% of total specimens ($n = 1177$). Mean (±1 s.d.) daily predator abundance in pan trap samples (701 pan trap hours

per plot) was 0.9 ± 1.5 on control plots and 3.9 ± 9.6 on experimental plots. Mean (±1 s.d.) daily parasitoid abundance in pan trap samples was 3.0 ± 3.4 on control plots and 5.1 ± 3.3 on experimental plots. Predator abundance (RM-ANOVA: $F_{6,42} = 6.40$, $p < 0.001$, generalized eta-squared effect size (ges) = 0.33) and parasitoid abundance (RM-ANOVA: $F_{6,42} = 5.13$, $p < 0.001$, ges = 0.29) in pan traps (pooled experimental and control plots) declined significantly over the study period.

The two top-performing models in the predator abundance (pan trap) candidate model set were statistically indistinguishable ($\Delta AIC_c < 2$) and accounted for 67% of the total model weight (electronic supplementary material, table S2). The top-performing model in the parasitoid abundance (pan trap) candidate model accounted for 56% of the total model weight (electronic supplementary material, table S3). Treatment had a significant effect on predator and parasitoid abundance in pan trap samples (table 2). Both predator and parasitoid abundance in pan traps were higher on experimental plots relative to control plots (figure 4*a*,*b*). The interaction between treatment and sampling day was not retained in any of the top-performing candidate models for predator or parasitoid abundance in pan traps (electronic supplementary material, tables S2 and S3). The abundance of Formicidae (GLS: $z = 3.47$, $p < 0.001$), Ichneumonoidea (GLS: $z = 2.82$, $p = 0.005$), Chalcidoidea (GLS: $z = 2.55$, $p = 0.011$) and Diaprioidea (GLS: $z = 1.98$, $p = 0.047$) in pan trap samples was higher on experimental plots relative to control plots (figure 4*c*). Full taxa-specific results from pan traps are provided in the electronic supplementary material, table S4.

The most-commonly sampled taxa in Malaise traps were Diptera ($n = 2878$), Lepidoptera ($n = 2005$) and Hymenoptera ($n = 1720$), representing 89% of total specimens ($n = 7418$). Mean (± 1 s.d.) daily predator abundance in Malaise trap samples (1413 Malaise trap hours per plot) was 0.7 ± 0.7 on control plots and 0.9 ± 0.7 on experimental plots. Mean (± 1 s.d.) parasitoid abundance in Malaise trap samples was 3.3 ± 2.7 on control plots and 3.2 ± 2.6 on experimental plots. Over the study period, parasitoid abundance in Malaise traps (pooled experimental and control plots) decreased significantly (RM-ANOVA: $F_{15,105} = 7.49$, $p < 0.001$, ges = 0.44) and predator abundance increased significantly (RM-ANOVA: $F_{15,105} = 3.78$, $p < 0.001$, ges = 0.30).

The two top-performing models in the predator abundance (Malaise trap) candidate model set were statistically indistinguishable ($\Delta AIC_c < 2$) and accounted for 63% of the total model weight (electronic supplementary material, table S5). The four top-performing models in the parasitoid abundance (Malaise trap) candidate model set accounted for 58% of the total model weight (electronic supplementary material, table S6). Full candidate model sets are provided in the electronic supplementary material. Predator abundance was significantly higher on experimental plots relative to control plots (table 3; figure 4*d*). Treatment was not retained in any of the top-performing candidate models for parasitoid abundance (electronic supplementary material, table S6) and we found no significant difference between treatments (figure 4*e*). The abundance of Araneae (spiders) (GLS: $z = 2.94$, $p = 0.003$) and Lepidoptera (moths) (GLS: $z = 2.21$, $p = 0.03$) in Malaise trap samples were higher on experimental plots relative to control plots (figure 4*f*). Full taxa-specific results from Malaise traps are provided in the electronic supplementary material, table S7.

**Table 2.** Conditional model-averaged parameter estimates (± adjusted s.e.), 95% confidence intervals (CI) and summed Akaike weights ($w_i$) for each parameter included in the candidate linear model set examining the effects of ALAN on arthropod predator and parasitoid abundance sampled in pan traps at the Hubbard Brook Experimental Forest, New Hampshire, USA. (Parameters were averaged across top-performing statistically indistinguishable ($\Delta AICc < 2$) candidate models. Global model: log (abundance) ~ treatment + block + study day + rainfall + study day × treatment. Parameters in italics have CIs that do not include zero.)

| response variable | parameter | estimate ± s.e. | CI | $w_i$ | $z$ | $p$ | effect[a] |
|---|---|---|---|---|---|---|---|
| predator abundance (pan traps) | intercept | −1.44 ± 0.19 | −1.81 −1.07 | — | — | — | — |
| | *block* (*north*) | 1.03 ± 0.22 | 0.60, 1.46 | 1.00 | 4.70 | *< 0.001* | +10.80 predators sampled per day on south plots |
| | *treatment* (*control*) | 0.62 ± 0.22 | 0.19, 1.05 | 0.89 | 2.81 | *0.005* | +4.14 predators sampled per day on experimental plots |
| | *study day* | −0.41 ± 0.14 | −1.41, −0.14 | 0.88 | 2.39 | *0.004* | −0.15 predators sampled per 1 day progression of study period |
| | *rainfall* | −0.32 ± 0.12 | −0.68, −0.13 | 0.71 | 2.86 | *0.011* | −0.31 predators sampled per 1 mm increase in rainfall |
| parasitoid abundance (pan traps) | intercept | −0.12 ± 0.13 | −0.38, 0.14 | — | — | — | — |
| | *treatment* (*control*) | 0.5 ± 0.15 | 0.20, 1.79 | 0.94 | 3.31 | *0.002* | +3.15 parasitoids sampled per day on experimental plots |
| | *block* (*north*) | 0.43 ± 0.15 | 0.14, 1.73 | 0.84 | 2.86 | *0.006* | +2.70 parasitoids sampled per day on south plots |

[a]Effect of 1-unit increase in numerical parameter in terms of response variable or the effect of categorical variable level in comparison to reference level.



royalsocietypublishing.org/journal/rspb *Proc. R. Soc. B* **290**: 20230153

**Table 3.** Conditional model-averaged parameter estimates (± adjusted s.e.), 95% confidence intervals (CI) and summed Akaike weights ($w_i$) for each parameter included in the candidate linear model set examining the effects of ALAN on predators and parasitoids sampled in Malaise traps at the Hubbard Brook Experimental Forest, New Hampshire, USA. (Parameters were averaged across top-performing statistically indistinguishable ($\Delta AIC_c < 2$) candidate models. Global model: log (abundance) ~ treatment + block + study day + rainfall + study day × treatment. Parameters in italics have CIs that do not include zero.)

| response variable | parameter | estimate ± s.e. | CI | $w_i$ | $z$ | $p$ | effect[a] |
|---|---|---|---|---|---|---|---|
| predator abundance (Malaise traps) | intercept | −0.30 ± 0.06 | −0.41, −0.18 | — | — | — | — |
| | *study day* | 0.15 ± 0.03 | 0.09, 0.22 | 1.00 | 4.67 | *< 0.001* | +0.10 predators sampled per 1 day progression of study period |
| | *treatment (control)* | 0.17 ± 0.06 | 0.05, 0.30 | 0.69 | 2.72 | *0.01* | +1.49 predators sampled per day on experimental plots |
| parasitoid abundance (Malaise traps) | intercept | 0.43 ± 0.06 | 0.32, 0.54 | — | — | — | — |
| | *study day* | −0.09 ± 0.03 | −0.16, −0.02 | 0.31 | 2.62 | *0.001* | −0.08 parasitoids sampled per 1 day progression of study period |
| | *temperature* | 0.08 ± 0.03 | 0.02, 0.18 | 0.38 | 2.71 | *0.01* | +0.55 parasitoids sampled per 1°C increase in temperature |
| | *rainfall* | −0.18 ± 0.04 | −0.25, −0.11 | 1.00 | 4.85 | *< 0.001* | −0.30 parasitoids sampled per 1 mm increase in rainfall |
| | *road (interior)* | −0.16 ± 0.06 | −0.28, −0.03 | 0.55 | 2.50 | *0.01* | −1.45 parasitoids sampled per day on plots adjacent to road |

[a]Effect of 1-unit increase in numerical parameter in terms of response variable or effect of categorical variable level in comparison to reference level.

## (c) Light intensity measurements

Daytime light environments (9.00 to 16.00) did not differ significantly between experimental and control plots (ANOVA: $F = 0.37$, $p = 0.55$) (electronic supplementary material, figure S1*a*). Lights illuminated experimental plots for approximately 5 h each night. HOBO data loggers were not effective at measuring low levels of illumination during the study period (levels below 40 lux were recorded intermittently, never below 5 lux). Mean (± 1 s.d.) reported night-time (21.00 to 24.00) lux was 0 ± 0 for control plots and 3.7 ± 6.1 for experimental plots. With measurements of 0 lux removed, the mean night-time lux for experimental plots was 12.2 ± 4.34 (electronic supplementary material, figure S1*b*). After the conclusion of the experiment, we tested for differences in nocturnal light environments between experimental and control plots by placing data loggers at different distances from a light source (0.5 m, 6 m (proxy for centre of experimental plot), and behind the light (proxy for control plot)) and recorded light intensity over three nights. At night, data loggers recorded 100–300 lux at 0.5 m and 0 lux behind the light source. The data logger at 6 m frequently logged 0 lux when the light was on at night, like results from data loggers during the study period. With these false zeros removed, this logger recorded a mean (±1 s.d.) lux of 11.6 ± 3.48 (electronic supplementary material, figure S1*c*). Thus, we estimate that clay caterpillars on experimental plots were exposed to between 10 and 15 lux of ALAN for approximately 5 h per night of our study.

# 4. Discussion

ALAN has increasingly been recognized as a threat to insect populations and communities [5], but most studies have focused on adult life stages with little known about the effects of ALAN on larvae. The results of this study provide experimental evidence that ALAN increases top-down pressure on caterpillars from arthropod predators and parasitoids. We found that predation rates (attacks) on clay caterpillars and the abundance of arthropod predators and parasitoids were higher on ALAN treatment plots than on control plots. Higher predation and parasitism pressure on caterpillars near light sources indicates that ALAN mediates changes in top-down control by arthropods and suggests potential consequences on caterpillar populations from nocturnal light pollution [23]. The mean proportion of clay caterpillars showing signs of predation was 9% higher on ALAN treatment plots than on control plots. Higher clay caterpillar predation on experimental plots probably occurred in part from the increased abundance of arthropod predators and parasitoids in response to the ALAN treatment. Although we did not directly test for other mechanisms, increased visibility of caterpillars under nocturnal illumination and the expansion of the temporal niche of arthropod predators and parasitoids could also have contributed to higher caterpillar predation rates on ALAN treatment plots [20].

The difference in clay caterpillar predation rate between experimental and control plots showed an increasing trend over the study period, although this trend was not statistically significant. This pattern was driven primarily by a decrease in predation rates on control plots while predation rates on experimental plots remained relatively constant over the study period. The seasonal decline in predation rates on artificial

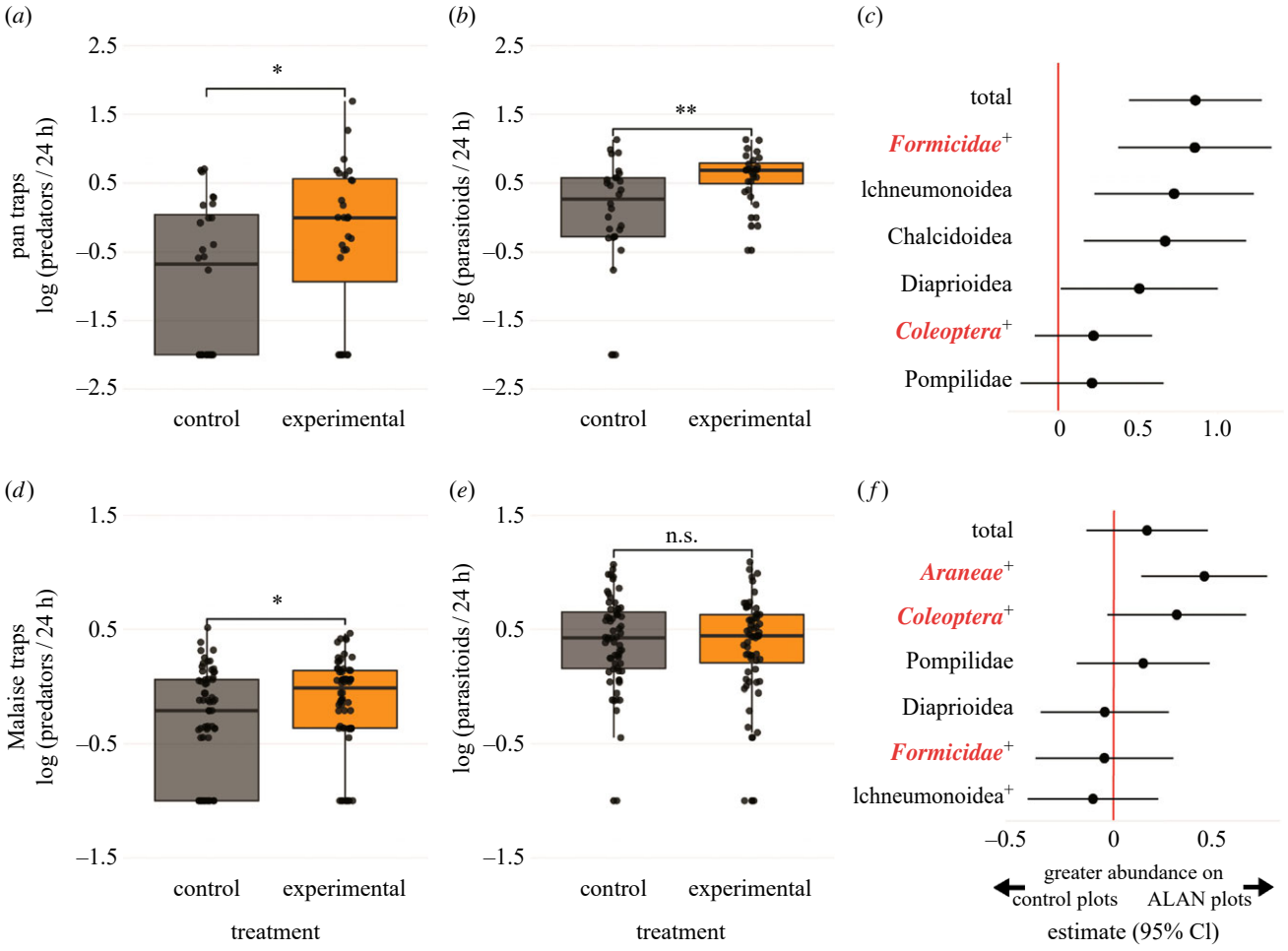


**Figure 4.** Mean abundance of (*a*) arthropod predators and (*b*) parasitoids in pan traps sampled on control and experimental plots at the Hubbard Brook Experimental Forest, New Hampshire, USA. Mean abundance of (*d*) arthropod predators and (*e*) parasitoids in Malaise traps sampled on control and experimental plots. Points represent individual samples with horizontal jitter. The box and midline represent the 25th, 50th and 75th quartiles; whiskers extend to the most extreme value within interquartile ranges beyond the 25th and 75th percentiles. Asterisks indicate significance at the $\alpha < 0.05$ (*) or $\alpha < 0.01$ (**) level (electronic supplementary material, table S4). Model estimates of the effect of ALAN treatment on abundance of predators and parasitoids in (*c*) pan traps and (*f*) Malaise traps. Estimates greater than 0 indicate higher abundance on experimental plots relative to control plots. Bars represent 95% confidence intervals (CI). Predatory taxa are indicated by red, italicized text. Possible sources of marks on clay caterpillar models are indicated by a plus sign '+'.

caterpillars on control plots might be explained by: (i) an overall decline in abundance of arthropod predators and parasitoids over the study period (catch rate of parasitoids decreased in Malaise and pan traps, catch rate of predators decreased in pan traps but increased slightly in Malaise traps), (ii) an increase in abundance of natural prey (Lepidopteran larvae) over the study period (electronic supplementary material, figure S2), and (iii) an increase in rainfall over the study period (electronic supplementary material, figure S3), which probably reduced arthropod activity. Notably, clay caterpillar predation rates on experimental plots remained relatively constant throughout the study period even while these other factors varied. This suggests that the impact of ALAN on the study system was strong enough to mask seasonal patterns in predation pressure resulting from changing ecological and weather factors. Future research should investigate how the impacts of ALAN interact with other environmental and ecological factors that regulate top-down pressure (e.g. temperature, lunar phase, population density of predators and prey).

Our findings on predation rates contribute to a growing understanding of ALAN's impacts on top-down pressure on arthropods [15,31], and to our knowledge, provide the first evidence of this impact on caterpillars. In contrast with our findings, a previous study that tethered live waxworm larvae found that ALAN did not significantly affect predation rates on larvae [29]. Their study was conducted in the Denver-Metro area, which has a higher level of background light pollution relative to Hubbard Brook [54]. Moreover, our study measured predation around newly established white LED lights rather than streetlights, which typically use low-pressure sodium bulbs that emit yellowish-orange light [4]. Brightness levels and the spectral signature of light sources influence the severity and directionality of ALAN impacts on species interactions [31,37] and the abundance and diversity of arthropods attracted to nocturnal light [55,56]. Additionally, because the response of arthropods to ALAN varies across taxa, the impact of ALAN probably depends on the arthropod community [57,58].

We recognize that clay caterpillars can only provide an estimate of the apparent predation rate on free-living caterpillars owing to their inherent differences. For example, predation rates measured with clay caterpillars can be biased by a lack of response from some predatory arthropods. Clay caterpillars do not have the same chemical signature as live caterpillars. Therefore, clay caterpillars more accurately measure the response of predators that use visual rather than chemical cues to find their prey. We attempted to reduce chemical

biases by punching holes in leaves where clay caterpillars were glued, releasing plant volatiles and mimicking leaf damage from caterpillar feeding. Additionally, clay caterpillars also do not exhibit anti-predation behaviours after detection such as dropping from leaves, which could lead to an overestimation of predation rate post-detection. The different biases in using dummy caterpillars may offset each other, producing an estimate of predation that does not differ significantly from the predation rate of live caterpillars [59]. Owing to these factors, we compared relative predation rates between treatments and across sampling periods rather than interpreting our results as exact measurements of caterpillar predation rates in the study system. Lastly, it is only possible to identify the attacks of potential predators on clay caterpillars at a coarse taxonomic level (bird, mammal, arthropod, etc). Classifying marks at a finer taxonomic level (e.g. Carabid versus Staphylinid beetle) is unreliable. However, concurrent arthropod sampling reduces some of this ambiguity by providing an overview of the predators and parasitoids present in the study area during the study period.

A variety of arthropods have been identified as 'predators' of clay caterpillars, including predatory stinkbugs (Pentatomidae), beetles (particularly Carabidae) and certain spiders (Araneae), but ants (Formicidae) and predatory wasps (e.g. Vespidae and Sphecidae) are often considered the primary predators [21,35,58]. Parasitoids do not frequently target caterpillar models, but a small number of ovipositor marks can occur—probably from larger Ichneumonid wasps [35]. We sampled spiders, predatory beetles, ants and Ichneumonid wasps on our study plots during the study period (figure 4*c*,*f*). Predatory wasps were not sampled in Malaise or pan traps during the study period but do occur in the study area. Only a few stink bugs were sampled, but these and other predatory Hemipterans are also found in the study area.

We documented different responses of the arthropod community to ALAN depending on the sampling method. While the abundance of arthropod predators was higher on experimental plots relative to control plots in both Malaise and pan traps, the abundance of parasitoids was only higher on experimental plots in pan traps. The disparity in parasitoid response between the two sampling methods can be explained by two related factors. Malaise and pan traps sample arthropods via different mechanisms—Malaise traps primarily work passively, intercepting insects in flight (although spiders use Malaise traps for structural support in web construction), while pan traps work actively, visually attracting insects to the bright colours [43]. Because pan traps rely on actively attracting insects, it is possible that the difference in parasitoid response to ALAN detected in pan and Malaise trap data reflects increased nocturnal activity of parasitoids on experimental plots relative to control plots [26]. Alternatively, these data might show different trends because of sampling biases inherent to the trap type [44]. Most taxa sampled in pan traps had significantly higher catch rates on experimental plots. By contrast, of taxa sampled in Malaise traps, only two taxa showed significant differences between treatments: Araneae (spiders) and Lepidoptera (moths), both of which had higher daily catch rates on experimental plots relative to control plots. Although pan traps and Malaise traps on our plots did sample different suites of taxa, we found considerable overlap, primarily among three Hymenopteran groups (Ichenumonoidea, Diaprioidea and Pompilidae (spider wasps)). The abundance of all three taxa were higher on experimental plots in pan trap samples but none showed a significant trend in Malaise trap samples. The difference between pan and Malaise trap data in this study highlights the importance of using multiple sampling methods to avoid incomplete or biased conclusions when examining the numerical response of arthropods to ALAN.

The data in this study on clay caterpillar predation and arthropod sampling were not separated into diurnal and nocturnal samples. This limits the conclusions we can draw about the mechanisms through which ALAN is hypothesized to impact top-down pressure on caterpillars, which differ for diurnal and nocturnal predation [20]. ALAN could increase nocturnal predation and parasitism pressure on caterpillars via the expansion of the temporal niche of arthropod predators and parasitoids (i.e. diurnal species foraging nocturnally) [26,27], increased visibility of caterpillars under nocturnal illumination for visual predators and parasitoids [1], and temporary aggregation of predators and parasitoids around light sources [3]. Whereas, diurnal predation could be impacted by a long-term increase in the density of predators and parasitoids around light sources [24]. Our finding that the sampled abundance of predators and parasitoids was higher on experimental plots suggests that the increase in predation could have been owing to increased nocturnal activity or a true increase in their density around light sources. Future studies should differentiate between diurnal and nocturnal predation to better understand the mechanisms underlying increased top-down pressure on caterpillars around light sources.

## 5. Conclusion

Given the global pervasiveness of ALAN, increased top-down pressure on caterpillars caused by ALAN could have population consequences for Lepidoptera. Increased predation and parasitism pressure on caterpillars from ALAN may act synergistically with the impacts of ALAN on adult life stages of Lepidoptera. Without additional research, however, the results from this study cannot be extrapolated to infer population-level impacts. In addition to the limited temporal duration of this study, the effects of ALAN vary with habitat and species and with the intensity and spectra of nocturnal lighting [31,60]. Nonetheless, reduced abundance of certain caterpillar species near light sources [23] and the implication of ALAN as a driver of moth population declines [61] stresses the need for further research to scale individual to population-level effects. The results of this study contribute to the growing body of evidence that ALAN impacts top-down pressure on arthropods and highlights the need for further research on the specific mechanisms by which ALAN impacts predation and parasitism in arthropods. A more detailed understanding of how ALAN impacts arthropods at all life stages will aid in the mitigation of negative impacts on arthropod biodiversity.

Data accessibility. Data and code for analysis are available from the Environmental Data Initiative repository: https://doi.org/10.6073/pasta/71525c9c724db0a21249584afca9ddbd [62].

Data are also provided in the electronic supplementary material [63].

Authors' contributions. J.F.D.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, writing—original draft and writing—review and editing; S.A.K.: conceptualization, funding acquisition, methodology, project administration, resources, supervision, writing—original draft and writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was supported by grants awarded to J.F.D. from the Rochester Academy of Science, the Society for Integrative and Comparative Biology, Cornell University College of Agriculture and Life Sciences, and the Cornell Laboratory of Ornithology Ivy Scholars Fund, which supports the Hubbard Brook Field Ornithology Program directed by S.A.K.

Acknowledgements. We thank Nina K. Lany (N.K.L.) and undergraduates from the laboratory groups of S.A.K. and David N. Bonter for feedback on earlier versions of this manuscript, Matthew P. Ayres and N.K.L. for lively discussions on experimental design, and Lindsey Forg for night photography of the study site. We thank Ian Halm for project logistics and Amey Bailey for early access to weather station data. This publication is a contribution of the Hubbard Brook Ecosystem Study. Hubbard Brook is part of the Long-term Ecological Research (LTER) network, which is supported by the U.S. National Science Foundation. Hubbard Brook Experimental Forest is operated and maintained by the U.S. Department of Agriculture, Forest Service, Northern Research Station.

## References


1. Desouhant E, Gomes E, Mondy N, Amat I. 2019 Mechanistic, ecological, and evolutionary consequences of artificial light at night for insects: review and prospective. *Entomol. Exp. Appl.* **167**, 37–58. (doi:10.1111/eea.12754)
2. Perkin EK, Hölker F, Tockner K. 2014 The effects of artificial lighting on adult aquatic and terrestrial insects. *Freshw Biol.* **59**, 368–377. (doi:10.1111/fwb.12270)
3. Owens ACS, Lewis SM. 2018 The impact of artificial light at night on nocturnal insects: a review and synthesis. *Ecol Evol.* **8**, 11 337–11 358. (doi:10.1002/ece3.4557)
4. Kyba CC *et al.* 2017 Artificially lit surface of Earth at night increasing in radiance and extent. *Sci Adv.* **3**, e1701528. (doi:10.1126/sciadv.1701528)
5. Owens ACS, Cochard P, Durrant J, Farnworth B, Perkin EK, Seymoure B. 2020 Light pollution is a driver of insect declines. *Biol. Conserv.* **241**, 108259. (doi:10.1016/j.biocon.2019.108259)
6. Hölker F, Wolter C, Perkin EK, Tockner K. 2010 Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **25**, 681–682. (doi:10.1016/j.tree.2010.09.007)
7. Van Geffen KG, Van Eck E, De Boer RA, Van Grunsven RHA, Salis L, Berendse F, Veenendaal EM. 2015 Artificial light at night inhibits mating in a Geometrid moth. *Insect Conserv. Divers.* **8**, 282–287. (doi:10.1111/icad.12116)
8. Van Geffen KG, Groot AT, Van Grunsven RHA, Donners M, Berendse F, Veenendaal EM. 2015 Artificial night lighting disrupts sex pheromone in a noctuid moth: moth sex pheromone in illuminated nights. *Ecol. Entomol.* **40**, 401–408. (doi:10.1111/een.12202)
9. Van Geffen KG, Van Grunsven RHA, Van Ruijven J, Berendse F, Veenendaal EM. 2014 Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecol. Evol.* **4**, 2082–2089. (doi:10.1002/ece3.1090)
10. Van Langevelde F, Van Grunsven RHA, Veenendaal EM, Fijen TPM. 2017 Artificial night lighting inhibits feeding in moths. *Biol. Lett.* **13**, 20160874. (doi:10.1098/rsbl.2016.0874)
11. Knop E, Zoller L, Ryser R, Gerpe C, Hörler M, Fontaine C. 2017 Artificial light at night as a new threat to pollination. *Nature* **548**, 206–209. (doi:10.1038/nature23288)
12. Macgregor CJ, Pocock MJO, Fox R, Evans DM. 2015 Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecol. Entomol.* **40**, 187–198. (doi:10.1111/een.12174)
13. Svensson AM, Rydell J. 1998 Mercury vapour lamps interfere with the bat defence of tympanate moths (Operophteraspp.; Geometridae). *Anim. Behav.* **55**, 223–226. (doi:10.1006/anbe.1997.0590)
14. Minnaar C, Boyles JG, Minnaar IA, Sole CL, Mckechnie AE. 2015 Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. McKenzie A, editor. *J. Appl. Ecol.* **52**, 522–531. (doi:10.1111/1365-2664.12381)
15. Mcmunn MS *et al.* 2019 Artificial light increases local predator abundance, predation rates, and herbivory. *Environ. Entomol.* **48**, 1331–1339. (doi:10.1093/ee/nvz103)
16. Kehoe R, Sanders D, Cruse D, Silk M, Gaston KJ, Bridle JR, Van Veen F. 2020 Longer photoperiods through range shifts and artificial light lead to a destabilizing increase in host–parasitoid interaction strength. *J. Anim. Ecol.* **89**, 2508–2516. (doi:10.1111/1365-2656.13328)
17. Sanders D, Kehoe R, Tiley K, Bennie J, Cruse D, Davies TW, Frank Van Veen FJ, Gaston KJ. 2015 Artificial nighttime light changes aphid-parasitoid population dynamics. *Sci. Rep.* **5**, 15232. (doi:10.1038/srep15232)
18. Manfrin A, Singer G, Larsen S, Weiß N, Van Grunsven RH, Weiß NS, Wohlfahrt S, Monaghan MT, Hölker F. 2017 Artificial light at night affects organism flux across ecosystem boundaries and drives community structure in the recipient ecosystem. *Front. Environ. Sci.* **5**, 61. (doi:10.3389/fenvs.2017.00061)
19. Kalinkat G, Grubisic M, Jechow A, Grunsven RHA, Schroer S, Hölker F. 2021 Assessing long-term effects of artificial light at night on insects: what is missing and how to get there. *Insect Conserv. Divers.* **14**, 260–270. (doi:10.1111/icad.12482)
20. Boyes DH, Evans DM, Fox R, Parsons MS, Pocock MJO. 2020 Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle: light pollution and moth life cycles. *Insect Conserv. Divers.* **14**, 167–187. (doi:10.1111/icad.12447)
21. Heinrich B. 1979 Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. *Oecologia* **42**, 325–337. (doi:10.1007/BF00346597)
22. Seifert CL, Schulze CH, Dreschke TCT, Frötscher H, Fiedler K. 2016 Day vs. night predation on artificial caterpillars in primary rainforest habitats - an experimental approach. *Entomol. Exp. Appl.*. **158**, 54–59. (doi:10.1111/eea.12379)
23. Boyes DH, Evans DM, Fox R, Parsons MS, Pocock MJO. 2021 Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* **7**, eabi8322. (doi:10.1126/sciadv.abi8322)
24. Davies TW, Bennie J, Gaston KJ. 2012 Street lighting changes the composition of invertebrate communities. *Biol. Lett.* **8**, 764–767. (doi:10.1098/rsbl.2012.0216)
25. Davies TW, Bennie J, Cruse D, Blumgart D, Inger R, Gaston KJ. 2017 Multiple night-time light-emitting diode lighting strategies impact grassland invertebrate assemblages. *Glob. Change Biol.* **23**, 2641–2648. (doi:10.1111/gcb.13615)
26. Gomes E, Rey B, Débias F, Amat I, Desouhant E. 2021 Dealing with host and food searching in a diurnal parasitoid: consequences of light at night at intra- and trans-generational levels. *Insect Conserv. Divers.* **14**, 235–246. (doi:10.1111/icad.12477)
27. Frank KD. 2009 Exploitation of artificial light at night by a diurnal jumping spider. *Peckhamia* **78**, 1–3.
28. Warren AD. 1990 Predation of five species of Noctuidae at ultraviolet light by the western yellowjacket (Hymenoptera: Vespidae). *J. Lepidopterists Soc.* **44**, 32. (doi:10.18473/lepi.69i1.a2)
29. Grenis K, Tjossem B, Murphy SM. 2015 Predation of larval Lepidoptera in habitat fragments varies spatially and temporally but is not affected by light pollution. *J. Insect Conserv.* **19**, 559–566. (doi:10.1007/s10841-015-9777-2)
30. Miller CR, Barton BT, Zhu L, Radeloff VC, Oliver KM, Harmon JP, Ives AR. 2017 Combined effects of night warming and light pollution on predator–prey interactions. *Proc. R. Soc. B* **284**, 20171195. (doi:10.1098/rspb.2017.1195)
31. Sanders D, Kehoe R, Cruse D, Van Veen FJF, Gaston KJ. 2018 Low levels of artificial light at night strengthen top-down control in insect food web.

*Curr. Biol.* **28**, 2474–2478.e3. (doi:10.1016/j.cub.2018.05.078)

32. Grenis K, Murphy SM. 2019 Direct and indirect effects of light pollution on the performance of an herbivorous insect. *Insect Sci.* **26**, 770–776. (doi:10.1111/1744-7917.12574)
33. Schwarz PA, Fahey TJ, Mcculloch CE. 2003 Factors controlling spatial variation of tree species abundance in a forested lanscape. *Ecology* **84**, 1862–1878. (doi:10.1890/0012-9658(2003)084[1862:FCSVOT]2.0.CO;2)
34. Van Doorn NS, Battles JJ, Fahey TJ, Siccama TG, Schwarz PA. 2011 Links between biomass and tree demography in a northern hardwood forest: a decade of stability and change in Hubbard Brook Valley, New Hampshire. *Can. J. For. Res.* **41**, 1369–1379. (doi:10.1139/x11-063)
35. Stange EE, Ayres MP, Bess JA. 2011 Concordant population dynamics of Lepidoptera herbivores in a forest ecosystem. *Ecography* **34**, 772–779. (doi:10.1111/j.1600-0587.2010.06940.x)
36. Lany NK, Ayres MP, Stange EE, Sillett TS, Rodenhouse NL, Holmes RT. 2016 Breeding timed to maximize reproductive success for a migratory songbird: the importance of phenological asynchrony. *Oikos* **125**, 656–666. (doi:10.1111/oik.02412)
37. Davies TW, Bennie J, Inger R, Ibarra NH, Gaston KJ. 2013 Artificial light pollution: are shifting spectral signatures changing the balance of species interactions? *Glob. Change Biol.* **19**, 1417–1423. (doi:10.1111/gcb.12166)
38. Howe A, Lövei GL, Nachman G. 2009 Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. *Entomol. Exp. Appl.* **131**, 325–329. (doi:10.1111/j.1570-7458.2009.00860.x)
39. Seifert CL, Lehner L, Adams MO, Fiedler K. 2015 Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south-western Costa Rica. *J. Trop. Ecol.* **31**, 281–284. (doi:10.1017/S0266467415000012)
40. Vieira EA, Arruda R, Massuda KF, Cardoso-Gustavson P, Guimarães EF, Trigo JR. 2019 Volatiles released by damaged leaves of *Piper mollicomum* (Piperaceae) act as cues for predaceous wasps: evidence using plasticine dummies as herbivore model. *Arthropod-Plant Interact.* **13**, 593–601. (doi:10.1007/s11829-019-09695-y)
41. Leuenberger W, Cohen JB, Rustad L, Wallin KF, Parry D. 2021 Short-term increase in abundance of foliage-gleaning insectivorous birds following experimental ice storms in a northern hardwood forest. *Front. For. Glob. Change* **3**, 142. (doi:10.3389/ffgc.2020.566376)
42. Low PA, Sam K, Mcarthur C, Posa MRC, Hochuli DF. 2014 Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. *Entomol. Exp. Appl.*. **152**, 120–126. (doi:10.1111/eea.12207)
43. Montgomery GA, Belitz MW, Guralnick RP, Tingley MW. 2021 Standards and best practices for monitoring and benchmarking Insects. *Front. Ecol. Evol.* **8**, 579193. (doi:10.3389/fevo.2020.579193)
44. Aguiar AP, Santos BF. 2010 Discovery of potent, unsuspected sampling disparities for Malaise and Möricke traps, as shown for Neotropical Cryptini (Hymenoptera, Ichneumonidae). *J. Insect Conserv.* **14**, 199–206. (doi:10.1007/s10841-009-9246-x)
45. Goulet H, Huber JT. 1993 *Hymenoptera of the world: an identification guide to families*, p. 668. Ottawa, Canada: Centre for Land and Biological Resources Research.
46. Johnson NF, Triplehorn CA. 2005 *Borror and DeLong's introduction to the study of insects*, 7th edn. Belmont, CA: Thomson Brooks/Cole.
47. Zuur A, Ieno AN, Walker N, Saveliev AA, Smith GG. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer. (doi:10.1007/978-0-387-87458-6)
48. Anderson DR, Burnham KP. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
49. Bartoń K. 2020 MuMIn: multi-model inference (R package). See https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.
50. R Core Team. 2022 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https://www.r-project.org/.
51. Pinheiro JS *et al.*. 2022 Nlme: linear and nonlinear mixed effects models (R package). See https://CRAN.R-project.org/package=nlme.
52. Zeileis A, Grothendieck G. 2021 zoo S3: infrastructure for regular and irregular time series. See https://CRAN.R-project.org/package=zoo.
53. Hair Jr JF, Black WC, Babin BJ, Anderson RE. 2010 *Multivariate data analysis*, 7th edn. Upper Saddle River, NJ: Prentice Hall.
54. Falchi F, Cinzano P, Duriscoe D, Kyba CCM, Elvidge CD, Baugh K, Portnov BA, Rybnikova NA, Furgoni R. 2016 The new world atlas of artificial night sky brightness. *Sci. Adv.* **2**, e1600377. (doi:10.1126/sciadv.1600377)
55. Justice MJ, Justice TC. 2016 Attraction of insects to incandescent, compact fluorescent, halogen, and led lamps in a light trap: implications for light pollution and urban ecologies. *Entomol. News* **125**, 315–326. (doi:10.3157/021.125.0502)
56. Van Langevelde F, Ettema JA, Donners M, Wallisdevries MF, Groenendijk D. 2011 Effect of spectral composition of artificial light on the attraction of moths. *Biol. Conserv.* **144**, 2274–2281. (doi:10.1016/j.biocon.2011.06.004)
57. Van Grunsven RHA, Becker J, Peter S, Heller S, Hölker F. 2019 Long-term comparison of attraction of flying insects to streetlights after the transition from traditional light sources to light-emitting diodes in urban and peri-urban settings. *Sustainability* **11**, 6198. (doi:10.3390/su11226198)
58. Pan H, Liang G, Lu Y. 2021 Response of different insect groups to various wavelengths of light under field conditions. *Insects* **12**, 427. (doi:10.3390/insects12050427)
59. Sam K, Remmel T, Molleman F. 2015 Material affects attack rates on dummy caterpillars in tropical forest where arthropod predators dominate: an experiment using clay and dough dummies with green colourants on various plant species. *Entomol. Exp. Appl.* **157**, 317–324. (doi:10.1111/eea.12367)
60. Larsson M, Göthberg A, Milberg P. 2020 Night, light and flight: light attraction in Trichoptera. *Insect Conserv. Divers.* **13**, 296–302. (doi:10.1111/icad.12379)
61. van Langevelde F *et al.* 2018 Declines in moth populations stress the need for conserving dark nights. *Glob. Change Biol.* **24**, 925–932. (doi:10.1111/gcb.14008)
62. Deitsch JF, Kaiser SA. 2023 Data and code from Artificial light at night increases top-down pressure on caterpillars: experimental evidence from a light-naive forest, 2021–2022. *Environ. Data Initiat.*. (doi:10.6073/pasta/71525c9c724db0a21249584afca9ddbd)
63. Deitsch JF, Kaiser SA. 2023 Artificial light at night increases top-down pressure on caterpillars: experimental evidence from a light-naive forest. Figshare. (doi:10.6084/m9.figshare.c.6440235)