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Severe and widespread reductions in night-time activity of nocturnal moths under modern artificial lighting spectra

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Artificial lighting has many negative impacts on nocturnal insects, from harmful phototaxis to disruption of feeding and reproduction. Although comparatively poorly explored, many detrimental outcomes could be associated with changes in activity. We investigated the effects of different types of light-emitting diode (LED) lighting on activity in multiple wild-caught moth species in three different families. While behaviour under natural conditions varied among species, artificial lighting strongly and largely consistently suppressed activity. In our main experiment, testing 843 moths of 23 species, we found that white LEDs at 10 lx illuminance depressed activity by 85% on average relative to natural night-time illumination, and even purportedly less harmful amber lighting had similar impacts at the same intensity. There were no differences between the effects of broad-spectrum LEDs and combinations of narrowband LEDs that produce equivalent light for human vision. Collection methods, using light traps or hand-catching with nets, did affect activity in some species, with implications for future research. Finally, further experiments found significant activity suppression overall under lighting at 1 lx, for white LEDs especially, with some species affected even by skyglow levels of white light. Substantial inhibition of activity under multiple streetlight-relevant LEDs suggests potential for widespread impacts on moth populations.

1. Introduction

Artificial light at night is a globally widespread and growing source of pollution, with extensive impacts on humans, wildlife and whole ecosystems [1,2]. Because of their infamous attraction to light, broad ecological and evolutionary diversity, and the availability of high-quality, long-term monitoring data, nocturnal moths (Lepidoptera) have long been a key focus for research into the effects of artificial light [3]. Understanding these impacts is increasingly important, given recent dramatic declines in insect populations around the globe [4], and growing concern that light pollution could be a contributing factor [5]. Within Lepidoptera, several studies report associations between greater declines and nocturnality, attraction to light or prevalence in light-polluted areas [6–8], alongside crucial evidence that long-term exposure to artificial lights can reduce moth abundance [9]. So far, much of the research on how moths respond to artificial lights has focused on characterizing the striking phenomenon of flight-to-light, or positive phototaxis [3]. Yet many other behavioural changes are observed when moths are exposed to lights [10,11]. Investigating these diverse responses is essential for a more comprehensive understanding of the potential consequences of light pollution for moth populations, as well as for designing more effective mitigation strategies.

In particular, artificial lights disrupt fundamental natural light cycles, daily, lunar and seasonal, that regulate essential processes such as circadian rhythms, diel activity and phenology across the tree of life [12,13]. Effects on daily activity patterns are especially well supported, with both diurnal and nocturnal species known to shift the timings of their activity in response to artificial light [14]. The behavioural patterns of nocturnal moths are strongly influenced by night-time illumination [15,16], and artificial light is recognized to have an inhibitory effect on moths [3,17]; as enthusiasts and collectors can attest, moths attracted to lights often stop flying and remain where they land for long periods, sometimes through the following day [18,19]. While readily observed, this behaviour has received relatively little research attention. Aside from some evidence in hawkmoths [20], the impacts of lighting on moth activity have been best explored in the context of pest management: several studies have demonstrated that yellow or green lighting can depress activity and so reduce crop damage by fruit-piercing Erebidae, as well as Crambidae and Noctuidae crop pests [21]. The effectiveness of these strategies across multiple moth families suggests a highly conserved response to light, widespread across the phylogeny of Lepidoptera. Yet the effects of more broad-spectrum lights, realistic to actual outdoor lighting regimes, have not been systematically tested. This represents an important knowledge gap, as activity inhibition has the potential for far-ranging consequences on moth populations. Activity suppression may increase predation risk for moths attracted to lights [18], as well as cause sublethal effects on fitness, by interfering with essential behaviours such as reproduction [22] and feeding [23].

Considering how different types of outdoor lights may affect activity is particularly timely, as lighting technology is undergoing a global shift from traditional light sources to light-emitting diodes (LEDs). As systems that produce amber light, such as high- and low-pressure sodium lamps (HPS and LPS), are replaced with whiter LEDs, this technological revolution is associated with striking changes in the spectral composition, or colour, of night-time lighting [24]. White LEDs emit a high proportion of short wavelengths of light, to which many species vulnerable to disruption by artificial lighting, including nocturnal moths, are especially sensitive [25]. This suggests that deploying white LED lights at scale could worsen the impacts of artificial light on ecosystems, although comparisons of moth phototaxis between LEDs and other light types are somewhat equivocal [3]. Regardless of spectrum, the greater efficiency and lower running costs of LEDs have also caused a rebound effect, encouraging greater use of outdoor lighting overall [2]. Yet LEDs also present opportunities for mitigating the impacts of artificial lighting, if used more judiciously [26,27]. LEDs produce more directional light, reducing spillover to areas where lighting is not needed [27], and can be spectrally tuned and combined in different ways to meet the requirements of human vision while avoiding wavelengths that are harmful to other species [26]. This includes producing amber light, generally considered less impactful on wildlife and less attractive to most nocturnal insects [28]: direct-emission, narrowband amber LEDs have spectra resembling those of LPS lamps, with similar effects on moth visual systems [29], while phosphor-converted (PC) amber LEDs use a reddish phosphor to convert nearly all the shortwave emissions from blue LEDs into longer wavelengths, producing a light spectrum with a broad amber peak [30]. These broadband amber lights in particular have been suggested as a viable, more ecologically sensitive alternative to white light, because they still support partial colour discrimination in humans [31]. Alternatively, if white light is needed, it can be generated by combining several narrowband monochromatic LEDs with red, blue and green (RGB) emissions [32], to reduce the overlap between emission spectra and visual sensitivities. Recent studies suggest that white light from these combinations of RGB LEDs may be less disruptive to insects than equivalent broad-spectrum LEDs [11,33].

Here, we measured activity in 843 wild-caught adult moths of 23 species, from three families (Erebidae, Geometridae and Noctuidae), under natural night-time lighting and when exposed to different LED technologies: broad-spectrum white LEDs, broad (PC) and narrowband amber LEDs, and combinations of narrowband RGB LEDs producing white and amber light. To maximize ecological relevance, adult moths were collected from the wild using both light traps and butterfly nets, allowing us to sample species with a range of responses to light; experiments took place outdoors, under natural night-time conditions, and moth activity was monitored throughout the night. Assessing the relative effects of multiple streetlight-relevant lights on a basic behavioural process across a broad range of species yields valuable insights into the possible impacts of proposed lighting regimes on nocturnal moth communities, and the effectiveness of potential mitigation strategies.

2. Methods

(a) Experimental design

Experiments ran for a total of 124 nights from 25 May to 7 September 2023 and 8 May to 16 September 2024, in two locations on the grounds of the University of Exeter's Penryn campus (Cornwall, UK; 50°10′12″ N, 5°7′22.8″ W). Moths were either captured with light traps (primarily a 15 W actinic trap and 125 and 80 W mercury vapour traps) or caught at night with butterfly nets, on campus and in nearby private gardens. Light-trapped moths were collected in the morning and then stored individually in plastic pots with air holes, in an outbuilding or shaded outdoor location until the following night. Net-caught moths were temporarily housed in the same type of individual pot when caught, but then included on the same night, typically within 1 hour of capture. Any moths found not responsive, either after housing or at the end of the experimental trial, were excluded. A total of 887 moths of 23 species were collected, sampled among common and widespread species in the UK [34,35], sufficiently abundant in the local area (electronic supplementary material, table S1). From these, 44 moths were excluded from analysis, due to equipment failure or damage to the moth, yielding a final sample size of n = 843 individuals (see electronic supplementary material, table S2a and S2b). Experiments were approved by the University of Exeter's ethics committee (Application ID: 515517).

In all experiments, each moth was individually placed in a custom-built experimental chamber, lit from above by a specific light treatment, and its behaviour was recorded throughout the night using time-lapse photography. Chambers consisted of an upturned frustum cone (13 cm diameter at the base, 35 cm at the top, 18 cm high), with an opaque white Perspex base and a clear, UV-transparent lid. The sides were lined with a removable pattern, consisting of 12 coloured segments printed on waterproof paper in a randomized order; this was placed under fine black netting, to encourage moths to settle (see electronic supplementary material, figure S1, for details). Filming from above, commercially available security cameras (Argus 2E, Reolink, China) with built-in 850 nm infrared lights were set to record a time-lapse video with a frame every 10 s (2304 × 1296 px resolution). Moths were introduced into the chambers as early as possible after the end of nautical twilight and filmed until sunrise, based on times obtained from www.timeanddate.com for the closest town, Falmouth (UK). The following morning, moths were marked on one forewing with a silver permanent marker pen (Artline 999 XF; see [36]) to prevent them from being re-used in subsequent experiments, then released in the area where they were collected.

Experiments took place outdoors, so that moths experienced conditions as close to their natural environment as possible, and the control treatment was lit by the night-time sky. To protect the equipment from rain and reduce the build-up of condensation, each chamber was placed inside an aluminium frame (50 × 50 cm, 120 cm high) with a clear UV-transparent lid, and sides composed of a mix of blackout black and silver waterproof fabric, and clear Veggiemesh. Up to eight experiments were run simultaneously every night, with the frames positioned so that their opaque sides prevented any contamination between neighbouring light treatments. Each frame was randomly assigned an experimental chamber and one of eight possible light treatments. Alongside a dark control (with no lights), we tested the effect of lighting from three single LEDs—a standard white LED (CCT = 5986 K), narrowband amber LED (CCT = 1621 K) and broadband PC amber LED (CCT = 1743 K)—as well as RGB LEDs, sets of three narrowband single LEDs that combined to produce light matching either the white or the broadband amber LEDs, according to human vision (subsequently labelled as RGB white and RGB amber, respectively; see electronic supplementary material, figure S1). All lights were positioned to illuminate the entire experimental chamber; they were set to produce an illuminance of 10 ± 0.1 lx at the level of the chamber lid, along with two lower light levels of the broadband amber LED (1 ± 0.1 lx and 0.1 ± 0.01 lx), representing a range of conditions from immediately below a typical streetlight to high levels of skyglow (although all these light sources would appear as point sources to the moths) [37]. LEDs were controlled through a mobile phone with custom Python code and individually calibrated in a dark room using an open-source mini spectroradiometer with a sensitivity of 0.005 lx [38]. RGB LEDs were further set to match the emissions of single LEDs (Euclidean distance in the human CIE XYZ space < 1), by measuring their CCT and coordinates in the human CIE XYZ space with a spectroradiometer (JETI Specbos 1211-UV, JETI Technische Instrumente GmbH, Germany). Natural night-time conditions measured at the field sites with the same mini spectroradiometer [38], at the time moths were introduced into the chambers, were typically an order of magnitude darker than the lowest intensity light treatment (median illuminance = 0.0168 lx, inter-quartile range (IQR) = 0.0102–0.0332 lx, based on 111 measurements in total).

Additional experiments further investigated activity in five species under the same single LEDs at lower intensities, using a similar set-up (n = 83, see electronic supplementary methods and electronic supplementary material, table S2c, for sample sizes and details). All moths were caught at night using butterfly nets and filmed for 4 hours under natural lighting or a randomly assigned light treatment: white LED light at 10, 1 or 0.1 lx, and broadband or narrowband amber LEDs at 1 lx.

(b) Video analyses

Video footage was analysed in ImageJ [39] using a custom plugin; moth positions were recorded every minute by clicking on the moth thorax (or every 10 s for additional experiments with lower light levels). Moths were considered to have moved between video frames if the Euclidean distance between successive positions was ≥ 10 pixels. We verified that this approach does not bias results towards estimating more movement for larger moths (see electronic supplementary methods for details).

(c) Phylogenetic reconstruction

Chromosome-level reference genome assemblies generated by the Darwin Tree of Life project [40], available for all but two species (*D. truncata* and *C. trigrammica*), were downloaded from the International Nucleotide Sequence Database Collaboration (INSDC; electronic supplementary material, table S3). A maximum-likelihood tree was then inferred with IQ-TREE2 (v. 2.3.6) [41] using a concatenated alignment of the 4976 protein sequences from single-copy orthologues present in at least 90% of the genomes, identified using BUSCO (v. 5.7.1) [42]. See electronic supplementary methods for details and parameters. All nodes in the resulting tree had 100% support from bootstrapping with 1000 replicates. For Bayesian analyses, the phylogeny was converted to an ultrametric tree using the mean path lengths method [43] with the *chronoMPL* function in the 'ape' package (v. 5.7.1) [44].

(d) Statistical analyses

All statistical analyses were carried out in R v. 4.3.2 [45]. Activity was calculated as the percentage of video frames in which each moth moved, over the whole night or in hour-long blocks from 20.00 to 08.00.

The effect of lights on total activity was initially tested across all species, using a linear mixed-effects model with light treatment and several control variables (capture method (trap or net), collection location (campus or private gardens), year, moon phase, mean temperature, mean humidity and Julian day) as fixed effects, along with species and family-level random effects. For each experimental night, moon phase was quantified as the mean percentage of moon face illuminated, computed for the field site location with an extinction coefficient for sea level ($e = 0.28$), using the *calculateMoonlightStatistics* function in the package 'moonlit' [46]. Mean temperature and humidity were calculated from the start to the end of the filming period for each moth, based on measurements from a weather station on the university campus. Activity was square-root-transformed to meet model assumptions, and the significance of fixed effects was tested using likelihood ratio tests. Planned comparisons between the light treatments and the control, and between broad-spectrum LEDs and their RGB equivalents, were carried out with Tukey's post hoc tests, using the *glht* function in the package 'multcomp' [47]. Total activity per species for each treatment was highly skewed, so all species-level differences in activity are reported as the median values of differences between individual activity in a lit treatment and median activity in the control for that species.

To account for phylogenetic relationships between species, the association between the treatment and the total activity was also tested with a phylogenetic mixed model, using the package 'MCMCglmm' [48]. Based on previously published methods for analysing treatment effects across species [49], the model included a random effect representing the effects of phylogeny under a Brownian model of evolution; fixed effects were as in the main linear mixed-effects model (see electronic supplementary methods for details of model specifications). The Markov chain Monte Carlo chain was run for 13 million iterations, with a burn-in of 3 million and sampling every 5000 iterations. Trace plots and autocorrelation values of samples in the chain were inspected to verify model convergence. Reported parameter estimates and 95% credible intervals (CIs) represent the medians of the posterior distributions and 95% highest posterior density intervals, respectively. Post hoc tests for planned comparisons were carried out using the 'emmeans' package [50] to calculate estimated marginal means for each light treatment.

Species-level repeatability of overall activity in the control condition was calculated using the *rpt* function in the 'rptR' package [51], with a simple linear mixed-effects model including all the same control factors as the main model as fixed effects and species as a random effect, with a Poisson distribution, 1000 bootstrap replicates and link-scale approximation. Assumptions were checked by visual inspection of diagnostic plots for the corresponding generalized linear mixed-effects model. This model was also used to test for phylogenetic signal in overall activity in natural night-time conditions, by extracting the conditional modes for the estimates of species-level random effects. Phylogenetic signal in these values was then tested with the *phyloSignal* function in the 'phylosignal' package [52], according to Pagel's Lambda [53], although other methods in *phyloSignal* yielded identical results.

Species differences in activity patterns in the control condition were investigated using linear mixed-effects models, with hourly activity as the dependent variable, time, species and all other control variables as independent fixed effects, and moth family as a random effect. The moon phase was calculated for each hour, using the *calculateMoonlightIntensity* function in the package 'moonlit' [46]. Time was taken as an integer from 0 to 12, representing time intervals from 8 pm to 8 am, and fitted with a second-order polynomial in the model. The significance of the interaction between time and species was tested with a likelihood ratio test. A similar approach was taken to explore patterns of activity across species, with treatment and time allowed to interact as fixed effects, and moth species and family included as random effects. For activity patterns across species, data were restricted to combinations of species and light treatment with at least four individuals.

Finally, additional analyses involving smaller numbers of species were carried out using linear mixed-effects models and linear models, as appropriate. Impacts of lower light levels on total activity for five species were tested with a linear mixed-effects model with treatment and Julian day as fixed effects, and species as a random effect. Activity was square-root transformed as above. To investigate the impacts of capture method, data for three species that could be captured by both nets and light traps (*Dysstroma truncata* (Geometridae), *Hypena proboscidalis* (Erebidae) and *Noctua pronuba* (Noctuidae)), exposed to either control conditions or white LEDs at 10 lx, were extracted from the main dataset ($N_{\mathrm{TOTAL}} = 59$; $N_{D.truncata} = 24$, $N_{H.proboscidalis} = 19$, $N_{N.pronuba} = 16$, with a mean of five moths per combination of species, capture method and light treatment). A linear model was fitted, with species, treatment and capture method allowed to interact; the significance of the three-way interaction was tested using an ANOVA.

3. Results

(a) Activity patterns under natural conditions

Focusing on the control condition only, under natural night-time conditions, moth species differed in their overall activity levels, and these were repeatable for species ($R = 0.494$, CI = 0.236 to −0.679). There was no phylogenetic signal in the conditional modes of the random effects for species in a model of overall activity in the control, accounting for temperature, humidity, moon phase, year, capture method and location, and Julian day, suggesting that closely related species did not necessarily display similar levels of activity (Pagel's Lambda (λ) = 4.701×10^{-5}, $p = 1$). The least active species included the peppered moth *Biston betularia* (Geometridae), black arches *Lymantria monacha* (Erebidae) and silver Y *Autographa gamma* (Noctuidae), while among the most active were the uncertain *Hoplodrina octogenaria* and dun-bar *Cosmia trapezina* (Noctuidae), and the green carpet *Colostygia pectinataria* (Geometridae; see figure 1*c*, electronic supplementary material, figure S2). We also modelled hourly activity through the night, using a linear mixed-effects model with a second-order polynomial for time, interacting with species, alongside all other variables as for overall activity, and moth family as a random effect. The interaction between time and species was significant (linear mixed-effects model (LMM), $\chi^2 = 195.39$, d.f. = 44, $p < 0.001$), suggesting that patterns of activity also varied among species (see electronic supplementary material, figure S3). Notably, while some species were most active in the darkest hours of night (e.g. *Cabera pusaria*, *Peribatodes rhomboidaria*), many had prolonged activity into the morning—whether displaying U-shaped curves with higher activity at the start and end of the experiment (e.g. *Xestia xanthographa*, *Hemithea*

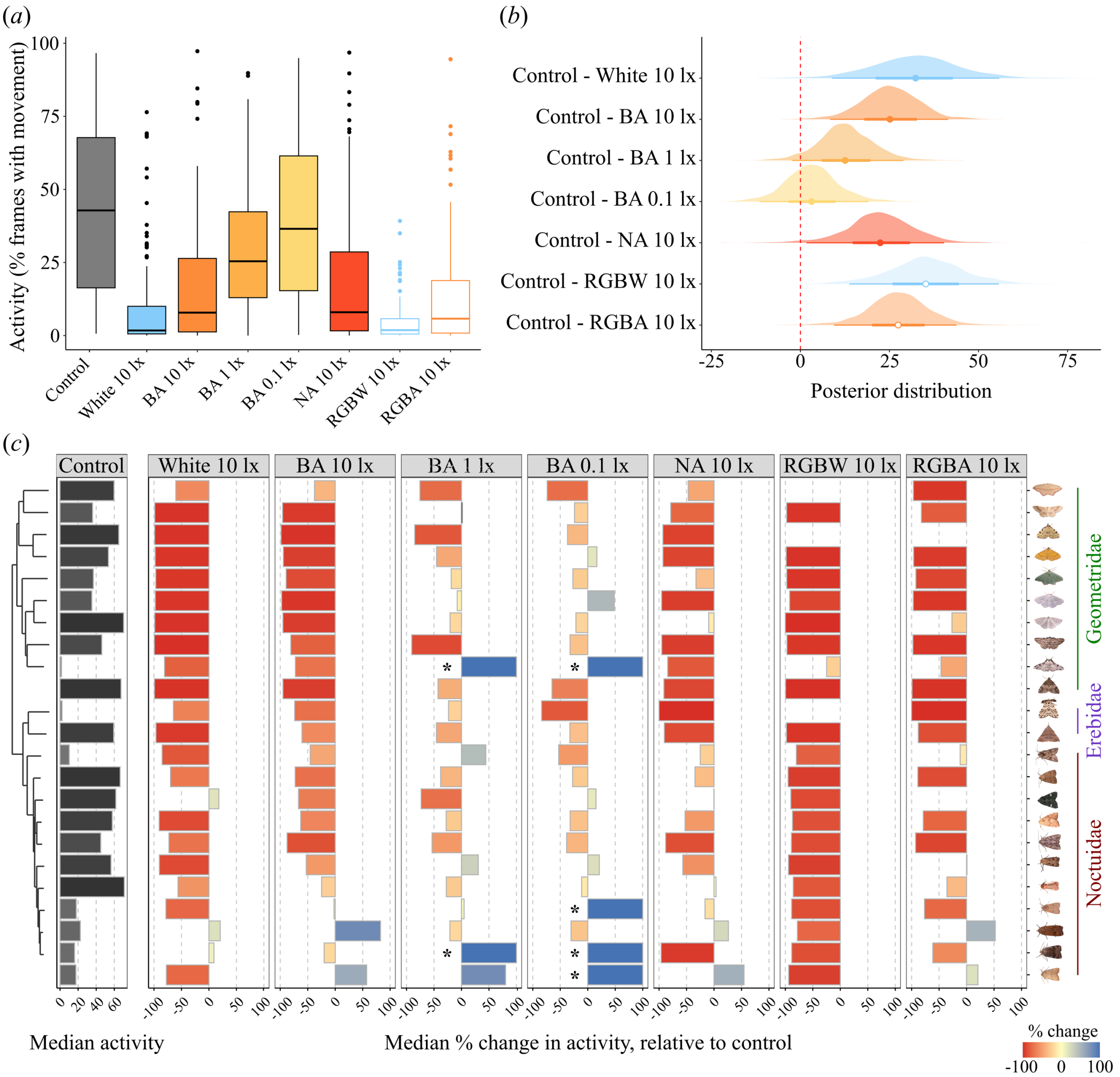

Figure 1. Effects of exposure to artificial light on total night-time activity. (*a*) Total activity across all 23 species and eight light treatments; boxplots represent the median and interquartile range (IQR), with whiskers set to 1.5 times the IQR. BA, broad amber; NA, narrow amber; RGB W, RGB white; RGB A, RGB amber LED. (*b*) Posterior distributions from the phylogenetic mixed model, for planned comparisons between control and lit treatments. Shading represents posterior distributions, circles median estimates for the distributions, thick lines 66% quantiles and thin lines 95% quantiles. Significant contrasts are expected when the 95th quantiles of the posterior distribution do not overlap with zero. (*c*) Species-level differences in activity (from top: *T. comae*, *I. aversata*, *C. pectinataria*, *C. bilenatum*, *H. aestivaria*, *C. margaritaria*, *C. pusaria*, *P. rhomboidaria*, *B. betularia*, *D. truncata*, *L. monacha*, *H. proboscidalis*, *A. gamma*, *H. octogenaria*, *M. persicariae*, *C. trapezina*, *A. monoglypha*, *A. exclamationis*, *O. plecta*, *X. xanthographa*, *N. pronuba*, *N. janthe*, *C. trigrammica*). Bar length and colour represent median activity per species in the control treatment (left-most panel) and median % change from the control in lit treatments (right panels). Increases in activity relative to the control were capped at 100% to facilitate visualization. Asterisks indicate cases where values exceeded 100%: actual percentage change was +240%, +137% for *B. betularia* and *N. janthe,* respectively, under broad amber lights at 1 lx, and +618%, +166%, +126%, +119% for *B. betularia*, *X. xanthographa*, *N. janthe* and *C. trigrammica,* respectively, under broad amber lights at 0.1 lx. Phylogenetic relationships are represented on the right, with branch lengths proportional to amino acid substitutions; species not included in the phylogeny are represented at the bottom of their respective families. Note that there are no data for *C. pectinataria* under RGB LEDs, *L. monacha* and *T. comae* under RGB white LEDs, or *M. persicariae* under RGB amber LEDs.

aestivaria), equal activity throughout (e.g. *Ochropleura plecta*, *Noctua janthe*) or even maximum activity in the early hours (e.g. *Noctua pronuba*).

(b) Effects of artificial light

Exposure to artificial light substantially reduced moth activity relative to the control. Across all species, without accounting for phylogeny, light treatment had a significant effect on overall night-time activity (LMM, $\chi^2 = 350.95$, d.f. = 7, $p < 0.001$); post hoc tests suggest exposure to all light types, barring the lowest level of broad amber LEDs (0.1 lx), led to significantly lower activity compared to natural night-time conditions (figure 1*a*; electronic supplementary material, table S4). When changes in activity between the control and light treatments at 10 lx were calculated per species, we recorded median declines in activity of 85, 73, 57, 93 and 82% under white, broad amber, narrowband amber, RGB white and RGB amber LEDs respectively, along with a 24% decline under broad amber LEDs at 1 lx only (figure 1*c*; electronic supplementary material, table S4). Depending on the specific

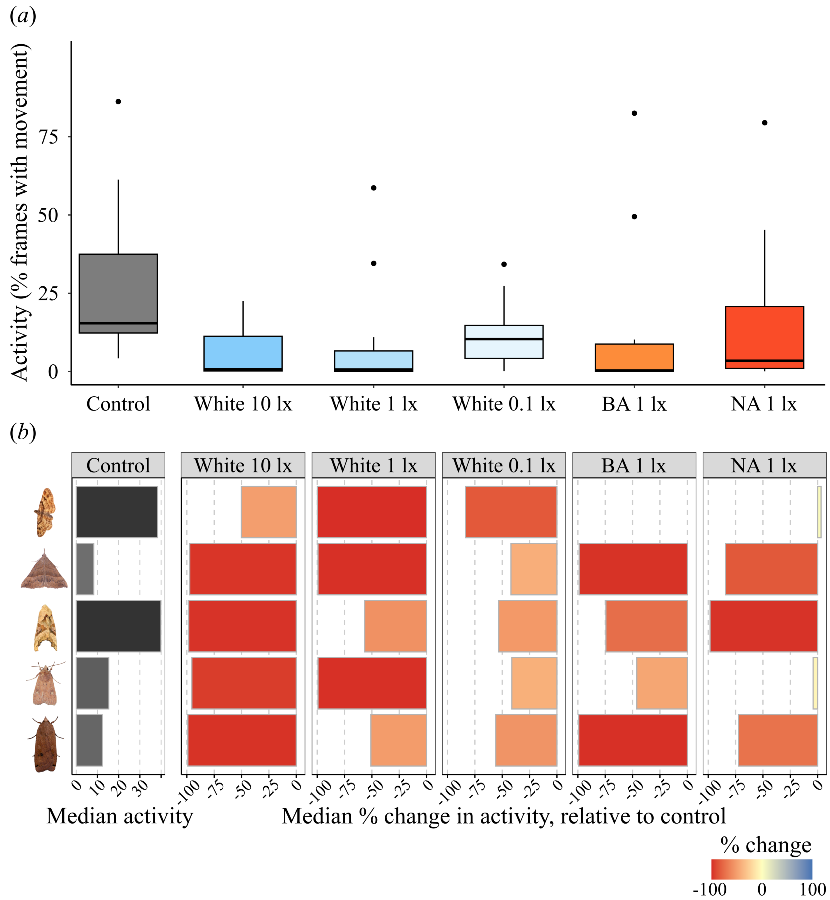

Figure 2. Effects of exposure to lower levels of artificial light on total night-time activity, in additional experiments with five moth species. (*a*) Total activity across all five species and six light treatments; boxplots represent the median and IQR, with whiskers set to 1.5 times the IQR. BA, broad amber; NA, narrow amber. (*b*) Species-level differences in activity (from top: *G. rufifasciata*, *H. proboscidalis*, *P. meticulosa*, *X. xanthographa*, *N. pronuba*). Bar length and colour represent median activity per species in the control treatment (left-most panel) and median % change from the control in lit treatments (right panels). There are no data for *G. rufifasciata* under broad amber LEDs at 1 lx.

treatment, 65–100% of the species tested had a lower median activity under lights than in the control condition (electronic supplementary material, table S4). In addition, there were no significant differences between the impacts of broad-spectrum white and amber LEDs and those of combinations of RGB LEDs with equivalent CCTs and intensities (Tukey's post hoc tests; $p_{\text{RGB white 10 lx – White 10 lx}} = 0.580$, $p_{\text{RGB amber 10 lx – Broad amber 10 lx}} = 0.917$). There were also small but significant effects of capture method, year and Julian day on activity levels: moths captured with light traps were less active than those caught with nets (LMM, estimate for traps = −0.719, $\chi^2 = 11.912$, d.f. = 1, $p < 0.001$), while moths were overall more active in 2024 than 2023 (LMM, estimate for 2024 = 0.593, $\chi^2 = 9.217$, d.f. = 1, $p < 0.01$), but activity declined slightly as the season advanced (LMM, estimate for Julian day = −0.0146 , $\chi^2 = 16.408$, d.f. = 1, $p < 0.001$). These trends remained significant even when data were restricted only to combinations of species and treatments with at least five individuals (electronic supplementary material, table S5).

Similar results were found using a phylogenetic mixed model with the 21 species for which phylogenetic information was available, suggesting that our conclusions regarding the impacts of artificial lighting are robust to different methods of inference. Posterior distributions from the model output suggested significant effects of light treatment, year and Julian day on total activity, replicating the trends found with non-phylogenetic analyses, but the effect of capture method was no longer significant (electronic supplementary material, table S6). Activity measurements were repeatable across all light treatments, with repeatability ranging from 0.210 under RGB white LEDs to 0.624 under narrow amber LEDs, and all CIs not overlapping with zero (electronic supplementary material, table S7). Post hoc tests found significant differences between the control and all light treatments at 10 lx, but not between the control and the lower levels of broad amber lighting (figure 1*b*; electronic supplementary material, table S8). As before, there was no difference between the impacts of broad-spectrum LEDs and their RGB equivalents (electronic supplementary material, table S8 and figure S4).

Finally, examining hourly activity through the night across all treatments also revealed a significant interaction between treatment and time (LMM, $\chi^2 = 28.159$, d.f. = 14, $p = 0.014$). While there is insufficient data to test a three-way interaction between treatment, time and species, examining actograms suggests that the effects of artificial lighting treatments on activity patterns do vary between species. In some species, the general pattern of activity could be maintained under different lights, except when activity was very severely suppressed overall; in others, such as *Noctua pronuba*, trends seen under control conditions were altered or even reversed under specific light types (see electronic supplementary material, figure S5).

Additional experiments investigating the effects of lower light intensities of the same single LEDs on a smaller number of species provide further support for a significant effect of light treatment on total night-time activity (LMM, $\chi^2 = 18.181$, d.f. = 5,

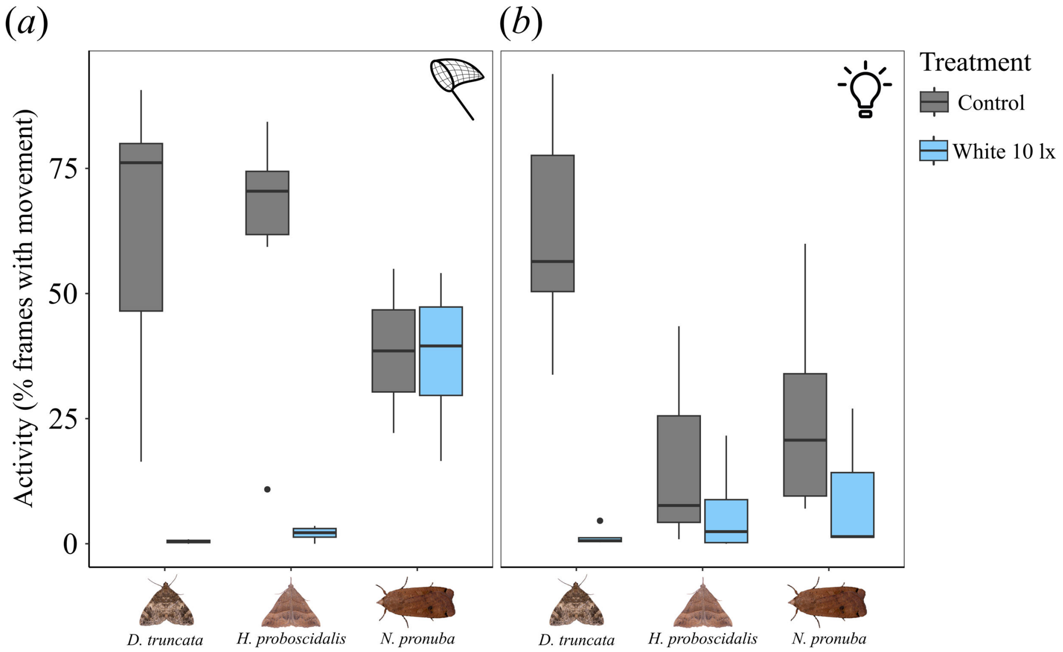

Figure 3. Night-time activity under control conditions and white LEDs for three species, captured using (*a*) nets or (*b*) light traps. Boxplots represent the median and IQR, with whiskers set to 1.5 times the IQR.

$p < 0.01$; figure 2*a*). In this case, however, there was no effect of Julian day (LMM, $\chi^2 = 2.393$, d.f. = 1, $p = 0.122$), presumably because these experiments were carried out over a shorter period. Post hoc tests suggest that white LEDs at intensities of both 10 and 1 lx led to significantly reduced activity compared to the control (Tukey's, $p < 0.01$ for both), as did broad amber LEDs at 1 lx (Tukey's $p = 0.0464$), while moth behaviour was not significantly affected overall under white LEDs at 0.1 lx, or narrow amber LEDs at 1 lx (Tukey's, $p = 0.246$ and $p = 0.214$, respectively). Nevertheless, comparing activity between lit and control treatments for each species suggests that many were still impacted by these lower light intensities, including white LEDs at an illuminance of just 0.1 lx, similar to skyglow levels of light pollution (figure 2*b*; electronic supplementary material, table S9).

(c) Effects of capture method

Finally, the effect of capture method on activity was further explored in three species exposed to either control conditions or white LEDs at 10 lx. Here, night-time activity was shaped by a significant three-way interaction between species, capture method and light treatment (ANOVA, $F_{2,42} = 3.583$, $p = 0.0366$), suggesting that capture method could not only affect overall activity but also modulate the impact of artificial lighting, and that these effects could vary between species (figure 3). For *D. truncata*, white lights strongly suppressed activity compared to the control, but the capture method had little effect on activity in either treatment. By contrast, light-trapped individuals of *N. pronuba* were on average 46% less active than net-caught ones in the control, and white light appeared to reduce activity further in light-trapped individuals only. Trends were different again for *H. proboscidalis*: all moths were relatively inactive under white lights, regardless of capture method, but activity in the control was on average 89% lower in light-trapped moths. As a result, using trap-caught moths of this species would suggest a smaller reduction of activity under white LEDs than would be estimated from moths caught with nets.

4. Discussion

With these experiments, we demonstrate severe impacts of artificial lighting on night-time activity in nocturnal moths. Activity was significantly suppressed under both white and amber light from LED technologies at an illuminance of 10 lx, across a range of species in three macro-moth families. Lower light intensities of white light also reduced activity, and some species were even affected by skyglow levels of illumination, suggesting that impacts of light pollution on moth activity are likely to be widespread. These results provide new insights into the potential efficacy of suggested mitigation strategies, such as altering the emission spectra of outdoor lights or reducing the intensity or duration of lighting [24,54].

As expected, white LED systems, rich in short wavelengths of light, were associated with the greatest and most consistent reduction in activity across species. Yet moths were still strongly inhibited by broad- and even narrowband amber lights, lacking these wavelengths, at the highest light intensity tested, suggesting that activity suppression is likely to be a much more pervasive response than might be predicted from studies of flight-to-light alone. This light level falls well within the range estimated below typical streetlights [37] and measured along UK hedgerows [55], so switching to amber lights would not mitigate the impacts of lighting on activity in many areas. Moreover, in contrast to recent findings in both moths and mosquitoes [11,33], we found no benefits of composite RGB LEDs compared to broad-spectrum single LEDs that appear identical to each other for humans. Just as the relative disruption caused by different light spectra can be highly taxon-specific [31], these findings highlight the importance of considering multiple behavioural contexts. Here, continuous night-time exposure to lights elicited different responses from studies of attraction [33] or flights past pulses of light [11], suggesting that the attractiveness of lights is not necessarily a good proxy for other impacts [3]. In Lepidoptera, multiple light types have been tested in other contexts beyond flight-to-light, such as feeding [23] and flower visitation [56], but determining the spectral responses for a wider range of behaviours would provide a fuller picture of the potential impacts of different lighting regimes.

Where identifying light spectra with minimal impacts is complex, reducing light intensity is more generally effective [31], and these mitigation strategies can be combined. In our main experiment, activity under broad amber lights at 1 lx and below was not significantly different from that seen under natural night-time lighting, when phylogeny was accounted for, suggesting that lower light levels were indeed less disruptive. Yet further tests with a smaller number of species did find a significant effect of white and even broad amber light at 1 lx, indicating that lower intensities still have the potential to be problematic. Effects of lower light levels were most consistent for white LEDs, suggesting that a combination of amber spectra and dimmer lights could be least harmful to nocturnal moths. Nevertheless, examining species-level changes in activity reveals substantial impacts of all dimmer lights tested on some species, even down to skyglow levels. As dim artificial light has been shown to affect the behaviour and activity patterns of nocturnal invertebrates [57,58], and skyglow is much more widespread globally than direct lighting [13], further investigation into the consequences of skyglow on moth activity would be worthwhile for assessing the wider impacts of light pollution.

A better understanding of the timings of activity in nocturnal Lepidoptera is also relevant for outdoor lighting. Moth species are known to vary in their patterns of activity, becoming active at different times as twilight progresses [59,60]. Monitoring behaviour throughout the night is therefore necessary to uncover the full effects of artificial lighting. This may also explain why activity suppression was not reported in experiments exposing greater wax moths *Galleria mellonella* to white LEDs for only a short time [61]; we also noticed that many moths were relatively active immediately after being introduced into the experimental chambers, as has been observed in hawkmoths in response to sudden transitions to light [62]. In line with previous work [59], we found repeatable species-specific differences in the patterns of activity displayed by moths under natural night-time conditions. In particular, many species remained active or even increased activity in the early hours of the morning and were least active in the darkest hours of the night. Equally, we captured individuals of most species on the wing during twilight, suggesting that they were also active earlier in the night. This has implications for the effectiveness of part-night lighting strategies: studies measuring the timings of insect aggregations at light find most insects reach lights within 3 hours after sunset [19,63], and similar patterns are found for early-emerging bat species [64,65], suggesting that switch-offs would need to be earlier than midnight to provide effective mitigation.

Light pollution may also be linked with shifts in the activity patterns of nocturnal moths. Such changes in the timings of behaviours are expected to have complex repercussions for ecological communities, shifting the balance of species interactions [66] through changes in the temporal and spatial overlap of predators and prey, increased competition between nocturnal and diurnal foragers, and mismatches between plant flowering and pollinator visits [62,67]. Experimental changes in photoperiod have been shown to affect activity patterns in hawkmoths [62], but it is unclear to what extent realistic artificial lighting scenarios might induce similar shifts. In this study, we found some evidence that light treatment did affect the shape of activity patterns throughout the night, but specific differences between lights could not be resolved, possibly due to insufficient data or because activity suppression was so severe. Moreover, moths were only introduced into the experimental chambers after the start of astronomical twilight, so we could not assess whether artificial lighting might delay the onset of activity during the crepuscular period. Future research could more explicitly test the effects of relatively low intensities of artificial light in modulating activity onset.

We also found evidence that the methods used for capturing moths from the wild could affect their activity levels. As species and sexes vary in their attraction to light [68,69], a combination of sampling techniques is required to capture a wide range of specimens. Yet differences between these methods are rarely explored (e.g. [59]). Here, we found that moths were overall less active when caught with light traps rather than nets, but only when phylogeny was not accounted for, suggesting that this was primarily explained by variation in species composition between methods. Nevertheless, further comparisons within species caught in both ways revealed that the capture method could, in some cases, modulate the impacts of artificial light, such that the detrimental consequences of lights could be masked by testing less active trap-caught moths. Recent research has raised awareness of the potential pitfalls of relying on light traps to monitor moth abundance and diversity [70,71], and our findings similarly emphasize the problems inherent in using artificial lights to collect individuals for experiments that go on to further test responses to light. In this case, there are several reasons why trap-caught moths may differ in their activity from net-caught individuals, including stress or damage from trapping and housing, differences in age, and species-, sex- and individual-level variation in responses to light. It would be interesting for future work to unpick the mechanisms driving differences between moths caught using light traps or other methods, but in the meantime, studies on moth behaviour should, where possible, account for potential biases introduced by collection methods [72].

Overall, our results suggest that activity suppression by artificial lighting is likely to be widespread and substantial and constitutes an important mechanism by which light pollution could contribute to moth population declines. An important caveat is that moths could not escape the light or seek refuge from it in our set-up, so future work should seek to measure the effects of lights on activity in more natural conditions. However, observations that moths can remain at lights for multiple days provide anecdotal evidence that the severe activity suppression we describe here can occur in the wild. In addition, measuring the effects of lights on activity, even in relatively artificial conditions, could still provide a useful and relatively straightforward assay to complement studies of flight-to-light. This would help build a more comprehensive picture of different species' vulnerability to disruption by lighting, enabling better predictions of downstream effects. Such tests could also help characterize effects on a broader range of less well-studied species, including micromoths or other nocturnal insects. In terms of mitigation strategies, our findings suggest that there is no single light type, intensity or timing of exposure that can fully alleviate the impacts of light pollution on moth activity, let alone when considering a broader range of species and impacts. Amber lighting, deployed at the lowest possible intensity, may have the least impact for nocturnal moths, but all LED systems likely to be considered for outdoor lighting will affect moth activity, highlighting the need to reduce light pollution overall and preserve dark skies where possible.

Ethics. Experiments were approved by the University of Exeter's ethics committee (Application ID: 515517).

Data accessibility. All data and code are provided in Dryad [73].

Supplementary material is available online [74].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.S.B.: conceptualization, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; J.A.M.G.: investigation, methodology, writing—review and editing; E.C.: investigation, writing—review and editing; C.J.W.: formal analysis, writing—review and editing; J.B.: conceptualization, funding acquisition, methodology, writing—review and editing; K.J.G.: conceptualization, funding acquisition, methodology, writing—review and editing; J.T.: conceptualization, funding acquisition, methodology, writing—review and editing.

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

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

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