

# A meta-analysis of biological impacts of artificial light at night

Dirk Sanders 10,1,2, Enric Frago 10,3,4, Rachel Kehoe<sup>2</sup>, Christophe Patterson<sup>2</sup> and Kevin J. Gaston 11,10,1

Natural light cycles are being eroded over large areas of the globe by the direct emissions and sky brightening that result from sources of artificial night-time light. This is predicted to affect wild organisms, particularly because of the central role that light regimes play in determining the timing of biological activity. Although many empirical studies have reported such effects, these have focused on particular species or local communities and have thus been unable to provide a general evaluation of the overall frequency and strength of these impacts. Using a new database of published studies, we show that exposure to artificial light at night induces strong responses for physiological measures, daily activity patterns and life history traits. We found particularly strong responses with regards to hormone levels, the onset of daily activity in diurnal species and life history traits, such as the number of offspring, predation, cognition and seafinding (in turtles). So far, few studies have focused on the impact of artificial light at night on ecosystem functions. The breadth and often strength of biological impacts we reveal highlight the need for outdoor artificial night-time lighting to be limited to the places and forms—such as timing, intensity and spectrum—where it is genuinely required by the people using it to minimize ecological impacts.

he development of electric lighting technology has transformed human societies, lengthening the time available for both work and pleasure<sup>1</sup>. Associated with human settlement, transport networks and industry, it has also profoundly altered the natural night-time environment. Large areas of the Earth now experience light that differs from natural regimes in timing, intensity and spectrum<sup>2,3</sup>. Nearly a quarter of the global land area already lies under artificially light-polluted night-time skies<sup>4</sup>. The area experiencing direct emissions from artificial light sources is estimated currently to be expanding at approximately 2% per annum, with localities that were previously lit brightening further at a similar rate<sup>5</sup>.

Artificial light at night (ALAN) is predicted to constitute a significant anthropogenic pressure on natural biological systems because (1) such systems are organized foremost by light, and particularly by daily and seasonal cycles of light and dark<sup>6–8</sup>, and (2) there have been no natural analogues, at any timescale, to the form, extent, distribution, timing or rate of spread of artificial lighting<sup>3</sup>. More obvious impacts like delayed retention of leaves on trees close to streetlights and attraction of insects and birds to outdoor lights, have long been documented<sup>9–11</sup>. However, particularly the last decade has seen rapid growth in the number of empirical studies testing for the impacts of ALAN on a broad array of biological phenomena across a wide diversity of organisms (for example, refs. <sup>12–16</sup>). Although there have been qualitative reviews of this literature<sup>2,17,18</sup>, quantitative analyses and understanding of the frequency and strength of the biological impacts of ALAN are lacking.

In this study, we report the results of a meta-analysis that takes into account the hierarchical structure of data due to the non-independence of several outcomes coming from the same study<sup>19,20</sup>, to build a quantitative understanding of the biological impacts of ALAN on a variety of responses from organisms and ecological communities. After a systematic search, we iden-

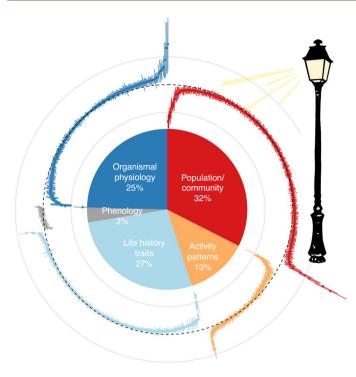
tified 126 publications from the peer-reviewed literature testing for the impacts of ALAN on organisms. Each individual measure was assigned to one of five major response categories: organismal physiology; seasonal phenology; life history traits; daily activity patterns; and population/community. The entire dataset covered a wide range of different measurements for each of the five categories and of different study organisms and habitats and included field and laboratory studies.

#### Results and discussion

Overall, the dataset was dominated by physiological, life history trait and population/community-based measures, ranging from strong negative to strong positive responses to ALAN exposure (Fig. 1). Thirty-five studies documented 338 observations reporting the impact on organismal physiology, 7 studies yielded 35 observations reporting the impact on organismal phenology, 58 studies reported 411 life history measures, 27 studies described 139 daily activity measures and 42 studies provided 381 observations of the impact on populations and ecological communities. We organized these measures into subcategories within each of the five main response categories (Methods and Fig. 2). This led to the exclusion of 196 measures from the analysis of subcategories because these were only included if they had measures from at least 5 different studies.

Regarding the physiological measures, the effect sizes for the hormone levels (mostly melatonin) indicated that these were consistently and markedly reduced across all studies included (Fig. 2b). By contrast, gene expression varied markedly in effect sizes, including a number of very strong positive responses (Fig. 2b). The impact on these two measures is important because this can have knock-on effects on other physiological parameters, such as health and alertness. The other three physiological measures (immune and stress responses and glands/structures) did not show an overall response to ALAN; however, the frequency distributions of effect sizes

<sup>1</sup>Environment and Sustainability Institute, University of Exeter, Penryn, UK. <sup>2</sup>Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, UK. <sup>3</sup>Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Centre de Biologie pour la Gestion des Populations, Montpellier, France. <sup>4</sup>Centre de Biologie pour la Gestion des Populations, Centre de Coopération Internationale en Recherche Agronomique pour le Développement, Institut National de la Recherche Agronomique, Institut de Recherche pour le Développement, Montpellier SupAgro, Université de Montpellier, Montpellier, France. <sup>⊠</sup>e-mail: k.j.gaston@exeter.ac.uk



**Fig. 1** | Physiological, phenological, life history trait, activity pattern and population/community-based responses to ALAN exposure. Single effect size measures (Hedges' d with 95% confidence interval) with responses from organismal physiology (blue), phenology (grey), life history traits (light blue), activity patterns (orange) and population/community (red) arranged in sequence according to increasing effect size (negative to positive). The circle dashed line indicates the zero effect size and the solid lines at effect sizes of 10 and -10. The pie chart indicates the proportion of measures belonging to each of the five categories.

for immune and stress responses (Fig. 2d-f) show that this does not mean that ALAN has no impact. Rather, depending on the conditions of the study, the response may be either positive or negative. For stress responses, the frequency distribution of effect sizes is bimodal, with peaks at low negative and higher positive values (Fig. 2e).

While single studies found evidence of phenological shifts in plants under ALAN exposure<sup>21</sup>, our dataset suggests that across plants and birds both positive and negative effect sizes for phenology have been documented (Fig. 2g), with no evidence for an overall consistent directional shift.

Among measures of life history traits (the term being used broadly), overall measures of cognition (mostly the performance of rodents in experimental tests) and offspring number were negatively impacted by ALAN; measures of predation were positively impacted (Fig. 2). Most conspicuously, and including some high effect sizes, measures of seafinding by young turtles (that is, the ability to find the right direction towards the sea) were regularly strongly impacted by ALAN (Fig. 2h), reflecting movement towards the (landward) light source. This has significant consequences for turtle survival, although the impact can be mitigated to some degree by careful design, positioning and shielding of lights<sup>22</sup>.

ALAN impacts were particularly marked for daily activity patterns with, overall, the onset of activity being pushed earlier and its cessation being delayed (Fig. 2). This did not manifest as an overall strong effect of ALAN on the duration of diurnal or nocturnal activity; however, in both cases the impacts were very varied and included strong positive and negative effect sizes (Fig. 2q,r). This highlights the diversity of influences of ALAN on different species,

increasing the duration of activity for some while reducing it for others<sup>23,24</sup> and acting as an attractor for some while as a repellent for others<sup>25</sup>. We looked in more detail at this directional variation for two animal groups, rodents and birds, which have been disproportionately well studied. For rodents, the duration of activity of both diurnal and nocturnal species tended to be reduced by exposure to ALAN (Fig. 3a). In contrast, for birds—with all of those included strictly diurnal—ALAN was more likely to lead to an extension of the duration of their activity, with onset and cessation of singing and foraging showing especially marked responses. This goes further in some groups, such that diurnal species can use the so-called 'night-time niche' to extend their activity into the night-time<sup>15</sup>.

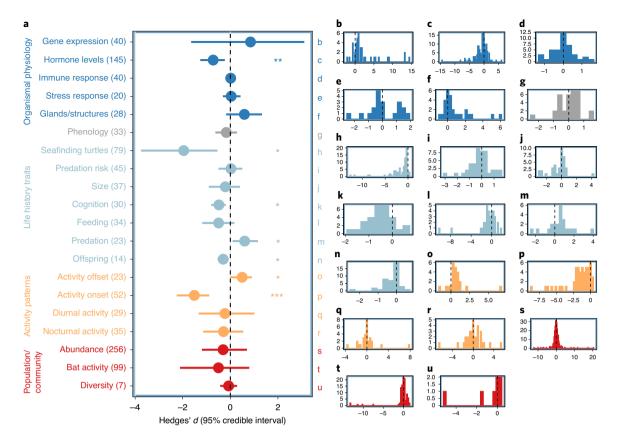
We found little evidence for a strong overall or net impact of ALAN on the abundance of species or the diversity of communities (Fig. 2). This outcome could potentially be explained as a consequence of the variation in, and possible trade-offs and synergies between, individual-level physiological, phenology, life history and activity responses. Indeed, abundance responses showed some of the greatest variation in effect sizes, from strongly negative to strongly positive, of any measured biological impacts of ALAN (Fig. 2s). For bats, for which the impacts of ALAN have attracted disproportionate scientific and policy attention<sup>26</sup>, activity (used as a measure of the presence or abundance of species rather than of the timing of individual movements) did not show an overall strong negative response (Fig. 2). However, while some effect sizes were positive, there was also a long tail of marked negative responses, highlighting that some bat species are strongly repelled by artificial light (Fig. 2t). Such complex patterns of responses may be typical of many taxonomic groups, with the overall response being driven by those species that are most dominant.

Species interactions are an important building block of ecological community structure. Predation, the most frequently studied interaction, was typically increased by ALAN exposure (Fig. 2m), indicating that interactions between species can be highly sensitive to ALAN and are key for understanding how whole communities are impacted (as shown in food webs<sup>15</sup> and pollination networks<sup>13</sup>). In turn, this likely leads to impacts of ALAN on ecosystem functions, but so far these have been little studied<sup>13,15</sup>; therefore, they could not be separately addressed in this meta-analysis.

ALAN might be predicted to impact nocturnal species more strongly than diurnal ones because the loss of light conditions (dark or light) under which organisms are active is probably more limiting than is their extension. There is evidence in our dataset that this is indeed the case. For life history and activity measures, the mean effect sizes were more negative for nocturnal species than for diurnal ones (Fig. 3b); however, there was a more negative response for physiological measures in diurnal species.

Overall, for most variables we did not find evidence for publication bias in effect sizes, in particular there was no evidence of P-hacking in any of the variables and no evidence of funnel plot asymmetry for most of them (Supplementary Table 1 and Supplementary Fig. 1). There was some statistical evidence for funnel plot asymmetry for hormone levels, seafinding by turtles and activity on and offset as well as for gene expression, gland structure and bat activity but these showed no strong overall directional effect size (Supplementary Table 1 and Supplementary Fig. 1). However, in all of these cases, this asymmetry may be driven by the biological nature of these responses rather than being the result of publication bias. For example, effect sizes for hormone levels predominantly concern the suppression of melatonin levels by artificial light, with overproduction being an unlikely outcome. Likewise, for seafinding in turtles, any diversion of movement from the direction of the sea is negative for the individuals concerned and results in a negative effect size; any normal movement would be regarded as an absence of effect (rather than a positive one).

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**Fig. 2 | Effect sizes for the measures from the main categories. a**, Effect sizes (Hedges' d) with post-mean and 95% credible intervals based on results from MCMCglmm for each variable from the five main categories (organismal physiology, phenology, life history traits, activity patterns and population/community). The numbers in brackets indicate the sample size and the asterisks the significance level for the pMCMC statistic, with \*P<0.05, \*P<0.01 and \*P<0.001). **b-u**, Histograms showing the distribution of the effect sizes for each of the categories shown in **a**, with the black dashed line indicating the zero P-axis intercept, the range of the effect size values on the P-axis and frequency on the P-axis.

Across the different studies, the levels of ALAN used in the experiments and observations were skewed towards low lighting of around 1-2 lx (such levels can occur approximately 10-20 m from an isolated streetlight) but covered the whole range up to 100 lx (similar to levels beneath stadium-type floodlighting), which we set as the upper limit for realistic ALAN exposure in nature. Lux is a measure of luminous flux per unit area based on human photopic vision but is typically used in studies of the biological effects of ALAN because it enables a direct link to illuminance as commonly measured in the environment and employed in the design and mitigation of artificial lighting systems. A meta-regression analysis found no relationship between the intensity of artificial light and effect size magnitude for the responses across all categories (Fig. 3c). Thus, while positive dose-response relationships have been documented for some individual physiological and behavioural responses to ALAN27, there is little evidence for an overall effect across a diversity of such responses. This is probably because of the wide variation in the form of dose-response relationships for individual biological responses to ALAN because in some cases no simple such relations exist and because of variation in spectral sensitivities. Consequently, the biological impact of even low intensities of ALAN may be marked 15,28.

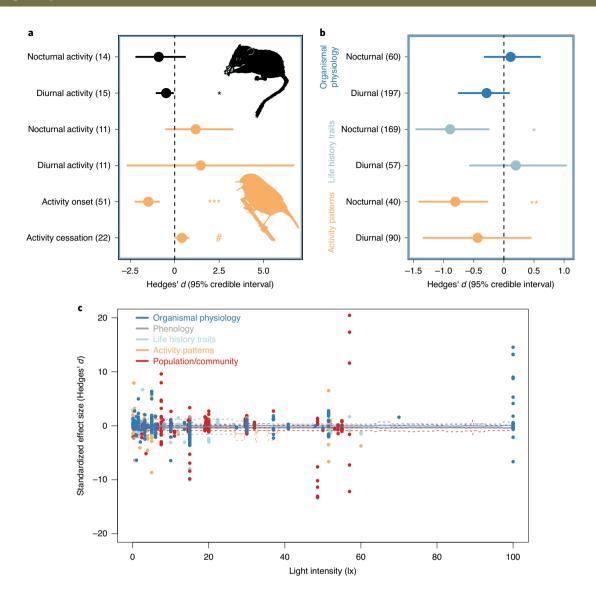
Notwithstanding the widespread nature of the biological effects of ALAN demonstrated by the results reported in this article, marked biases continue to exist in the taxonomic groups and regions for which empirical studies of these effects have been conducted. Of the 1,304 effect sizes included in the meta-analysis, 24 were for microbial communities, 143 for plants, 388 for invertebrates and 746 for vertebrates. The dataset includes almost double the number of field studies (82) compared to laboratory experiments (42), with

the majority of field studies in the meta-analysis from Europe (46), North America (17) and Australia (7). Tropical regions were markedly under-represented, despite the prediction that effects of ALAN could be particularly strong at low latitudes because of the limited natural seasonal variation in the lengths of daylight and night-time<sup>6</sup>. Further, more research is needed on the response of whole ecological communities and their functions to ALAN exposure<sup>29</sup>; the strong response of trophic behaviour to ALAN suggests that species interactions change and with them whole community structures and their functions will shift. Interactions with other human pressures, especially climate change, are of particular interest since for species that exploit the night-time niche their behaviour at night is often temperature-dependent.

#### **Conclusions**

The results reported in this article have significant implications for the much-discussed mitigation of the effects of ALAN on the natural environment<sup>30,31</sup>. First, they underline how widespread these effects are, including on diurnal species, and that where possible mitigation should be routine rather than limited to places and times when taxa perceived to be of particular concern (for example, bats) are active. Second, they highlight the challenge of making recommendations to regulate the maximum intensities of particular kinds of lighting, given that marked biological impacts of ALAN occur across a wide range of intensities including very low lighting levels (below 1 lx). Third, we show that ALAN especially changes the physiology and behaviour of organisms by affecting hormone levels, the onset of daily activity, feeding and phototaxis but typically with a less strong impact on particular community responses, such as abundance and

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**Fig. 3 | Activity patterns and light intensity. a**, Impact of ALAN on rodent and bird activity. Effect sizes (Hedges' d) with post-mean and 95% credible intervals based on the results from the MCMCglmm package for each variable. **b**, Impact of ALAN on diurnal and nocturnal species for the categories of organismal physiology, life history traits and activity patterns. **c**, Meta-regression of effect sizes and artificial light intensity levels for organismal physiology (blue), phenology (grey), life history traits (light blue), activity patterns (orange) and population/communities (red). The numbers in brackets indicate the sample size and the asterisks the significance level for pMCMC, with \*P<0.005, \*\*P<0.001, \*\*P<0.001, \*P<0.006).

species richness; this suggests that the impact on community structure and diversity might be less clear and depends on the impacts on key players (species or groups<sup>29</sup>). Although species richness was not systematically affected in our study, it is possible that ALAN is often altering community composition (that is, beta diversity) so that sensitive species are being replaced.

Concern has repeatedly been expressed about the impacts of the loss of natural night-time light cycles on humans that span from their physiology to their psychological sense of place<sup>9</sup>. In this study, we show that a broad array of marked impacts also occur on other organisms.

#### Methods

Literature search. We identified relevant literature using keyword searches in Web of Science (we used the 'All databases' option including Web of Science Core Collection, BIOSIS Citation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index and SciELO Citation Index) and Scopus, finding any available papers published until 22 October 2019. (We constrained our searches to these databases to focus on peer-reviewed studies and tested

for publication bias.) We used the terms: "TS=(('Artificial light\* at night' OR 'Light\* pollution' OR 'Light\* at night' OR 'night time light\*') AND ('species' OR 'ecosystem\*' OR 'ecological commun') AND ('abundance' OR 'behaviour' OR 'richness' OR 'reproduction' OR 'mating' OR '\*diversity' OR 'composition' OR 'predation' OR 'herbivory' OR 'activity' OR 'timing' OR 'physiology' OR 'flight to light\*' OR 'melatonin' OR 'development' OR 'trophic' OR 'biomass' OR 'pollination'))". After removing 352 duplicates, combining the searches resulted in 614 publications that were screened for the inclusion criteria. To be included in the meta-analysis, studies needed to (1) test for ALAN effects on organisms either in the field or the laboratory; (2) have a control group that was exposed to natural light levels at night (or a dark control) and treatment groups with exposure to ALAN up to 100 lx-studies with higher levels were excluded since these are unlikely to occur in the field; (3) have at least 2 replicates per treatment; and (4) contain data on means, estimation of variation and sample size. If only box plots were presented, we extracted the median and interquartile range<sup>32</sup>. This resulted in 126 papers, with a total of 1,304 effect size measures (refs. 12,1

Categorization of effect size. We categorized the effect size measures into five different main groups: response to exposure to ALAN of (1) organismal physiology, (2) phenology, (3) life history traits, (4) activity patterns (for example, daily diurnal, nocturnal activity) or (5) population/community. For the analyses,

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we were interested in which factors drive the response within each category. We selected subcategories within each of the five major categories that we thought described the dataset best. For each subcategory to be included in the analysis, it needed to have data that were extracted from at least five different studies. Below, we briefly explain the subcategories.

Organismal physiology. Several studies measured the impact of ALAN on the level of gene expression and hormones produced. We also included immune response and stress response. Gland structure includes the size of glands but also the size of structures adjacent to them and neuronal structures.

*Phenology.* This describes seasonal timings of events such as flowering dates in plants and egg-laying in birds (measured in Julian days).

Life history traits. Life history traits are traits that affect the life table of an organism and therefore its fitness. Based on the biology of the different species studied, the different effect sizes were classified as either having a positive or negative relationship with fitness. To express the fitness consequences of all effect sizes, effect sizes were multiplied by -1 when the relationship between the trait and fitness was negative. Thus, effect sizes larger than zero express a benefit for the organism, whereas the opposite is true for values lower than zero. A total of seven categories were considered: seafinding in turtles; predation risk; body size; cognition; feeding; predation; and reproductive output.

A large number of effect sizes concern sea turtles and their ability to find the sea after emerging from eggs or after egg-laying by females. Turtles are expected to reach the sea as fast as possible to avoid predation and other risks, so increased time or distance in doing so and large differences in the direction of a straight line between egg emergence or laying and the sea are considered as negatively related with fitness. Predation risk is a trait negatively related to survival, which has been measured in many ways. In this category, most effect sizes come from studies of pairwise predator-prey interactions. Predation risk has been measured as (the sign after each trait expresses whether the trait is positively or negatively associated with fitness): attacks suffered by prey (-); attack attempts by predators (-); activity of predators (-); anti-predatory behaviours shown by prey (+); and abundance of prey in response to experimental exposure to predators (+). Size has been considered as having a positive effect on fitness since larger individuals are usually more fecund and live longer. Although considered as an independent category, cognition strongly relates to feeding efficiency and survival because individuals with poor cognition are less likely to forage efficiently, escape predation and ultimately survive. Cognition has been measured with the following traits (the sign after each trait expresses whether the trait is positively or negatively related to fitness). In rodents, cognition has been measured as the time spent to escape from a maze (-) and in birds as the time to solve a cognition test (-). Indirect measures of cognition include measuring sleep debt by either estimating sleep debt directly on animals (-) or by estimating the concentration of oxalic acid in blood (that is, a molecule that signals sleep debt) (-). For primary consumers, the traits included are preference over the habitual food source, food consumption, time spent eating and food absorption efficiency. Reproduction includes reproductive output, but also pre- and post-reproductive behaviours.

Activity patterns. The data for daily activity patterns contain measures of when animals started or ceased their activity (mostly measured against sunrise and sunset) and the duration of their activity. This resulted in four subcategories: activity onset; activity cessation; diurnal activity duration; nocturnal activity duration. One study measured the time spent while inactive; this was included in activity duration by changing the sign of the effect size.

Population/community. This category mostly contained data on the abundance of single species and communities (groups of species, such as functional groups) in the presence and absence of ALAN. Bat density is usually estimated indirectly as the number of passes, a variable that does not really describe activity but an indication of abundance. A few studies looked at the species richness of communities (diversity).

Data analysis. The meta-analysis was conducted in R v.3.6.0 (ref.  $^{152}$ ) using the package metafor version 2.4-0  $^{153}$  to estimate the standardized mean difference (Hedges' d) and corresponding sampling variance for each data point using the 'escalc(measure = 'SMDH')' command. These values were then used to fit a meta-analytic model in MCMCglmm version 2.29  $^{19}$ . To achieve this, the random term idh(SE):units was fixed to one in the prior so that all measurement errors could be considered as independent of each other. In addition, to account for study-level non-independence due to multiple measurements per study, 'Study' was included as a random effect. The Markov chain Monte Carlo chain ran for 150,000 iterations and it was sampled every 50 iterations with the first 50,000 removed as burn-in to prevent autocorrelation among subsequent iterations. Autocorrelation between consecutive samples was always lower than 0.1 and convergence of the chains was inspected visually to ensure that there were no trends in the chain and that posterior distributions were not skewed. Significance is reported as the pMCMC statistic  $^{19,154}$ . Since we did not have any a priori knowledge on the distribution of our data, we

used a flat prior: the inverse-gamma prior (V=1, nu=0.002). Hedges' d was used to compare measures of the variables between treatment and control. We present the mean effect size and 95% credible intervals; the mean effect size was considered significantly different from 0 if its 95% confidence interval did not include 0.

Further, additional analyses used light intensity in lux as a moderator (equivalent to main effects in standard linear models).

**Testing for publication bias.** For all variables in the meta-analysis, we assessed evidence of publication bias. Publication bias implies that studies with low effect sizes were less likely to be published than studies with larger effect sizes15 However, these assumptions are not always valid and some authors have suggested that publication bias is mostly caused by significance levels and P-hacking<sup>156</sup>. The first form of bias was tested using asymmetry in funnel plots of meta-analytic residuals against the inverse of their precision (defined as 1/sampling variance)<sup>2</sup> For multilevel meta-analysis models, funnel plots based on meta-analytic residuals (the sum of effect size-level effects and sampling variance effects) are better suited than those based on effect sizes<sup>157</sup>. We interpreted asymmetry in funnel plots carefully given the small sample sizes for some of the variables, and the lack of bidirectional outcomes for light impact on some traits, which will inevitably lead to a biased plot. For example, for turtles, if there is an impact of exposure to ALAN on seafinding this will always be negative. Further, we ran Egger's regressions using the meta-analytic residuals as the response variable and precision as the moderator<sup>15</sup> If the intercept of the Egger's regression does not overlap zero, estimates from the opposite direction to the meta-analytic mean might be missing, which can be evidence of publication bias<sup>157</sup>. *P*-hacking was tested with the *P*-curve technique, which can provide evidence of P-hacking if values close to a significance level of 0.05 are over-represented in the data<sup>156,158</sup>. The *P*-curve was performed with the function peurve from the dmetar package version 0.0.9000159

**Reporting Summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

#### Data availability

All data generated or analysed during this study are available from the Dryad Digital Repository<sup>160</sup>.

#### Code availability

The computer code for the meta-analysis is available from the Dryad Digital Repository  $^{\rm 160}.$ 

Received: 7 September 2019; Accepted: 28 August 2020; Published online: 02 November 2020

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#### Acknowledgements

We thank A. Sánchez-Tójar, B. W. T. Coetzee and D. T. C. Cox for comments and discussions, and A. Voronkova for translations. This work was supported by a Natural Environment Research Council grant no. NE/N001672/1.

#### **Author contributions**

K.J.G. conceived the study. K.J.G. and D.S. designed the study. D.S., R.K. and C.P. extracted the data. E.F. and D.S. analysed the data. D.S., E.F., R.K. and K.J.G. prepared the manuscript.

### **Competing interests**

The authors declare no competing interests.

#### Additional information

 $\label{eq:Supplementary information} Supplementary information is available for this paper at $$https://doi.org/10.1038/s41559-020-01322-x.$ 

Correspondence and requests for materials should be addressed to K.J.G.

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Corresponding author(s):	Kevin J Gaston
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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.					
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The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement					
A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly					
The statistical test(s) used AND whether they are one- or two-sided  Only common tests should be described solely by name; describe more complex techniques in the Methods section.					
A description of all covariates tested	A description of all covariates tested				
A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons					
A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coe AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)	ull description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient). D variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)				
For null hypothesis testing, the test statistic (e.g. $F$ , $t$ , $r$ ) with confidence intervals, effect sizes, degrees of freedom and $P$ value noted Give $P$ values as exact values whenever suitable.					
For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings				
For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes					
Estimates of effect sizes (e.g. Cohen's <i>d</i> , Pearson's <i>r</i> ), indicating how they were calculated					
Our web collection on <u>statistics for biologists</u> contains articles on many of the points above.					
Software and code					
Policy information about <u>availability of computer code</u>					
Data collection Data were collected using literature search using Web of Science Database and Scopus.					
Data analysis Data analysis was done using the packages metafor and MCMCglmm for R version 3.6.0.					
For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/r We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.	eviewers.				
Data					

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All data generated or analysed during this study are included in this published article (and its supplementary information files).

Field-specific reporting					
<u>·</u>	v that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.				
Life sciences	Behavioural & social sciences				
For a reference copy of the docum	ent with all sections, see <u>nature.com/documents/nr-reporting-summary-flat.pdf</u>				
Ecological, evolutionary & environmental sciences study design					
All studies must disclose or	these points even when the disclosure is negative.				
Study description	To understand the impact of artificial light at night on physiology and behavior of organisms and ecological communities, we conduct a meta-analysis, following a systematic search.				
Research sample	We identified 126 publications from the peer reviewed literature testing for the impact of ALAN on organisms.				
Sampling strategy	We identified relevant literature using keyword searches in Web of Science (we used "All databases" including Web of Science Core Collection, BIOSIS Citation Index, KCI-Korean Journal Database, MEDLINE, Russian Science Citation Index and SciELO Citation Index) and Scopus, finding any available papers published until 22 October 2019 (we constrained our searches to these databases to focus on peer-reviewed studies, and tested for publication bias – see below). We used the terms: "TS= (("Artificial light* at night" OR "Light* pollution" OR "Light* at night" OR "night time light*") AND ("species" OR "ecosystem*" OR "ecological commun") AND ("abundance" OR "behaviour" OR "richness" OR "reproduction" OR "mating" OR "*diversity" OR "composition" OR "predation" OR "herbivory" OR "activity" OR "timing" OR "physiology" OR "flight to light*" OR "melatonin" OR "development" OR "trophic" OR "biomass" OR "pollination"))". After removing 352 duplicates, combining the searches resulted in 614 publications that were screened for inclusion criteria. To be included in the meta-analysis, studies needed to (1) test for ALAN effects on organisms either in the field or the lab; (2) have a control group that was exposed to natural light levels at night (or a dark control) and treatment groups with exposure to ALAN up to 100 lux - studies with higher levels were excluded as these are unlikely to occur in the field; (3) have at least 2 replicates per treatment; and (4) contain data on means, an estimation of variation and sample size. If only box plots were presented, we extracted the median and interquartile range. This resulted in 126 papers, with a total of 1304 effect size measures.				
Data collection	Data were extracted from publication using reported effect sizes, from figures and supplementary data files.				
Timing and spatial scale	Indicate the start and stop dates of data collection, noting the frequency and periodicity of sampling and providing a rationale for these choices. If there is a gap between collection periods, state the dates for each sample cohort. Specify the spatial scale from which the data are taken				
Data exclusions	No data were excluded from the overall presentation (Figure 1). We organised the extracted measures into subcategories within each of the five main response categories (Fig. 2). This led to the exclusion of 196 measures from the analysis of subcategories because these were only included if they had measures from at least five different studies.				
Reproducibility	All search and inclusion criteria are described in the manuscript, see above.				
Randomization	n/a				
Blinding	Three researchers were involved in the literature search and selection process, and compared their independent outcomes and discussed less obvious cases.				
Did the study involve field	r specific materials, systems and methods				
We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.					
Materials & experime	ental systems Methods				

Materials & experimental systems		Me	Methods	
n/a	Involved in the study	n/a	Involved in the study	
$\boxtimes$	Antibodies	$\boxtimes$	ChIP-seq	
$\boxtimes$	Eukaryotic cell lines	$\boxtimes$	Flow cytometry	
$\boxtimes$	Palaeontology	$\boxtimes$	MRI-based neuroimaging	
$\boxtimes$	Animals and other organisms			
$\boxtimes$	Human research participants			
$\boxtimes$	Clinical data			