



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

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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.

The development of electric lighting technology has transformed human societies, lengthening the time available for both work and pleasure¹. 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^{2,3}. Nearly a quarter of the global land area already lies under artificially light-polluted night-time skies⁴. 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 rate⁵.

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^{6–8}, and (2) there have been no natural analogues, at any timescale, to the form, extent, distribution, timing or rate of spread of artificial lighting³. 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^{9–11}. 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. ^{12–16}). Although there have been qualitative reviews of this literature^{2,17,18}, 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^{19,20}, 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

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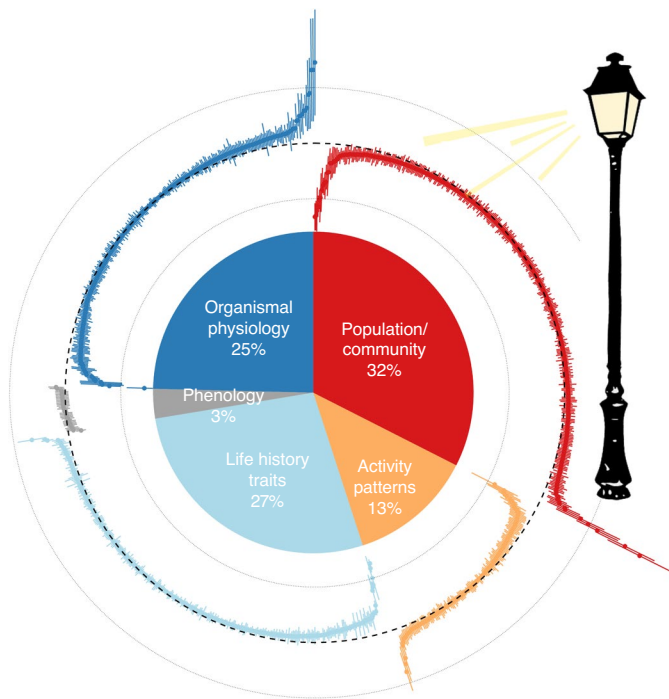


Fig. 1 | Physiological, phenological, life history trait, activity pattern and population/community-based responses to ALAN exposure. Single effect size measures (Hedges' d with 95% confidence interval) with responses from organismal physiology (blue), phenology (grey), life history traits (light blue), 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 exposure²¹, 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 lights²².

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^{23,24} and acting as an attractor for some while as a repellent for others²⁵. 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-time¹⁵.

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 attention²⁶, 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 webs¹⁵ and pollination networks¹³). In turn, this likely leads to impacts of ALAN on ecosystem functions, but so far these have been little studied^{13,15}; 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).

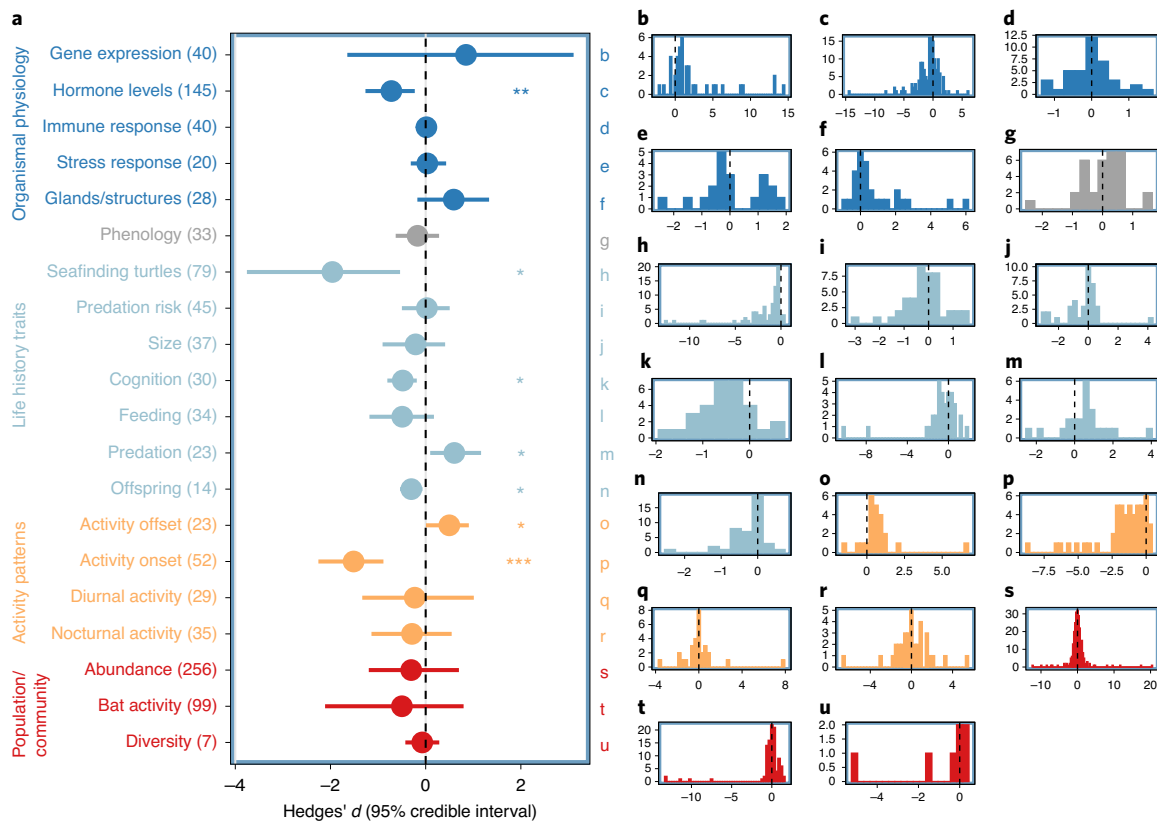


Fig. 2 | Effect sizes for the measures from the main categories. **a**, Effect sizes (Hedges' d) with post-mean and 95% credible intervals based on results from MCMCglmm for each variable from the five main categories (organismal physiology, phenology, life history traits, activity patterns and population/community). 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 x -axis intercept, the range of the effect size values on the x axis and frequency on the y 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-time⁶. Further, more research is needed on the response of whole ecological communities and their functions to ALAN exposure²⁹; 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^{30,31}. 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

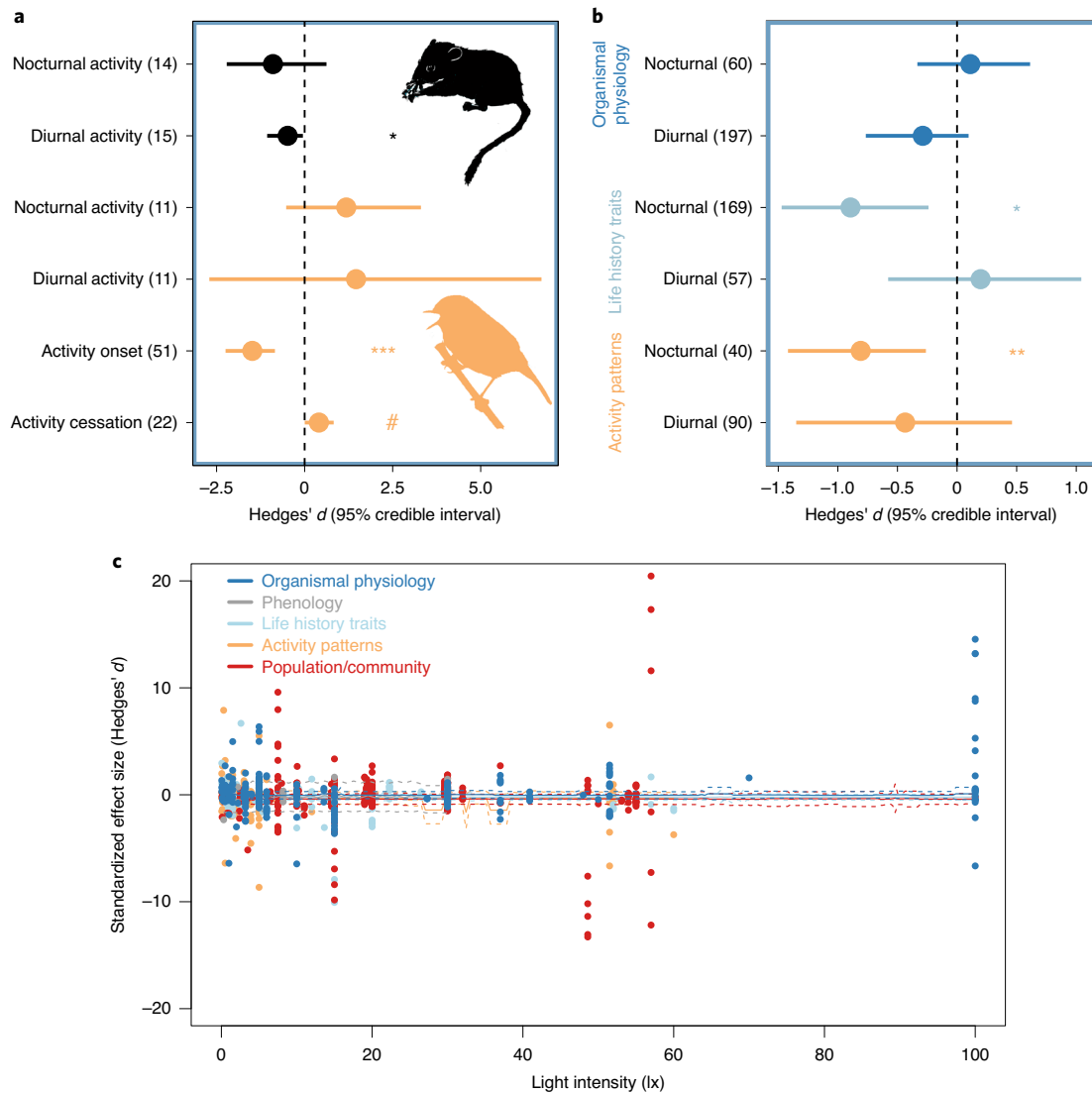


Fig. 3 | Activity patterns and light intensity. a, Impact of ALAN on rodent and bird activity. Effect sizes (Hedges' d) with post-mean and 95% credible intervals based on the results from the MCMCglmm package for each variable. **b**, Impact of ALAN on diurnal and nocturnal species for the categories 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 * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, # $P < 0.06$.

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 groups²⁹). 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 place⁹. 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 range³². This resulted in 126 papers, with a total of 1,304 effect size measures (refs. ^{12,13,15,16,25,27,28,33–151}).

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,

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.¹⁵³) using the package metafor version 2.4-0¹⁵³ 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 2.29¹⁹. 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 sizes¹⁵⁵. However, these assumptions are not always valid and some authors have suggested that publication bias is mostly caused by significance levels and P -hacking¹⁵⁶. The first form of bias was tested using asymmetry in funnel plots of meta-analytic residuals against the inverse of their precision (defined as $1/\text{sampling variance}$)³⁰. 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 sizes¹⁵⁷. 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 moderator¹⁵⁷. 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 bias¹⁵⁷. 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^{156,158}. The P -curve was performed with the function pcurve 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 Repository¹⁶⁰.

Code availability

The computer code for the meta-analysis is available from the Dryad Digital Repository¹⁶⁰.

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References

- Gaston, K. J., Gaston, S., Bennie, J. & Hopkins, J. Benefits and costs of artificial nighttime lighting of the environment. *Environ. Rev.* **23**, 14–23 (2015).
- Gaston, K. J., Bennie, J., Davies, T. W. & Hopkins, J. The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol. Rev. Camb. Phil. Soc.* **88**, 912–927 (2013).
- Gaston, K. J., Visser, M. E. & Hölker, F. The biological impacts of artificial light at night: the research challenge. *Phil. Trans. R. Soc. B* **370**, 20140133 (2015).
- Falchi, F. et al. The new world atlas of artificial night sky brightness. *Sci. Adv.* **2**, e1600377 (2016).
- Kyba, C. C. M. et al. Artificially lit surface of Earth at night increasing in radiance and extent. *Sci. Adv.* **3**, e1701528 (2017).
- Gaston, K. J., Davies, T. W., Nedelec, S. L. & Holt, L. A. Impacts of artificial light at night on biological timings. *Annu. Rev. Ecol. Evol. Syst.* **48**, 49–68 (2017).
- Kronfeld-Schor, N. & Dayan, T. Partitioning of time as an ecological resource. *Annu. Rev. Ecol. Evol. Syst.* **34**, 153–181 (2003).
- Bradshaw, W. E. & Holzapfel, C. M. Light, time, and the physiology of biotic response to rapid climate change in animals. *Annu. Rev. Physiol.* **72**, 147–166 (2010).
- Matzke, E. B. The effect of street lights in delaying leaf-fall in certain trees. *Am. J. Bot.* **23**, 446–452 (1936).
- Verheijen, F. J. The mechanisms of the trapping effect of artificial light sources upon animals. *Arch. Neerl. Zool.* **13**, 1–107 (1960).
- Howell, J. C., Laskey, A. R. & Tanner, J. T. Bird mortality at airport ceilometers. *Wilson Bull.* **66**, 207–215 (1954).
- Stone, E. L., Jones, G. & Harris, S. Street lighting disturbs commuting bats. *Curr. Biol.* **19**, 1123–1127 (2009).
- Knop, E. et al. Artificial light at night as a new threat to pollination. *Nature* **548**, 206–209 (2017).
- Van Doren, B. M. et al. High-intensity urban light installation dramatically alters nocturnal bird migration. *Proc. Natl Acad. Sci. USA* **114**, 11175–11180 (2017).

15. Sanders, D., Kehoe, R., Cruse, D., van Veen, F. J. F. & Gaston, K. J. Low levels of artificial light at night strengthen top-down control in insect food web. *Curr. Biol.* **28**, 2474–2478.e3 (2018).
16. Spoelstra, K., Verhagen, I., Meijer, D. & Visser, M. E. Artificial light at night shifts daily activity patterns but not the internal clock in the great tit (*Parus major*). *Proc. Biol. Sci.* **285**, 20172751 (2018).
17. Perkin, E. K. et al. The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere* **2**, 122 (2011).
18. Rich, C. & Longcore, T. *Ecological Consequences of Artificial Night Lighting* (Island Press, 2006).
19. Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* **33**, 1–22 (2010).
20. Sánchez-Tójar, A. et al. Meta-analysis challenges a textbook example of status signalling and demonstrates publication bias. *eLife* **7**, e37385 (2018).
21. Bennie, J., Davies, T. W., Cruse, D. & Gaston, K. J. Ecological effects of artificial light at night on wild plants. *J. Ecol.* **104**, 611–620 (2016).
22. Bertolotti, L. & Salmon, M. Do embedded roadway lights protect sea turtles? *Environ. Manage.* **36**, 702–710 (2005).
23. Russ, A., Rüger, A. & Klenke, R. Seizing the night: European blackbirds (*Turdus merula*) extend their foraging activity under artificial illumination. *J. Ornithol.* **156**, 123–131 (2015).
24. Threlfall, C. G., Law, B. & Banks, P. B. The urban matrix and artificial light restricts the nightly ranging behaviour of Gould's long-eared bat (*Nyctophilus gouldi*). *Austral Ecol.* **38**, 921–930 (2013).
25. Mathews, F. et al. Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Phil. Trans. R. Soc. B* **370**, 20140124 (2015).
26. Stone, E. L., Harris, S. & Jones, G. Impacts of artificial lighting on bats: a review of challenges and solutions. *Mamm. Biol.* **80**, 213–219 (2015).
27. Dominoni, D. M., Carmona-Wagner, E. O., Hofmann, M., Kranstauer, B. & Partecke, J. Individual-based measurements of light intensity provide new insights into the effects of artificial light at night on daily rhythms of urban-dwelling songbirds. *J. Anim. Ecol.* **83**, 681–692 (2014).
28. Brüning, A., Hölker, F., Franke, S., Kleiner, W. & Kloas, W. Influence of light intensity and spectral composition of artificial light at night on melatonin rhythm and mRNA expression of gonadotropins in roach *Rutilus rutilus*. *Fish Physiol. Biochem.* **44**, 1–12 (2018).
29. Sanders, D. & Gaston, K. J. How ecological communities respond to artificial light at night. *J. Exp. Zool. A Ecol. Integr. Physiol.* **329**, 394–400 (2018).
30. Falchi, F., Cinzano, P., Elvidge, C. D., Keith, D. M. & Haim, A. Limiting the impact of light pollution on human health, environment and stellar visibility. *J. Environ. Manage.* **92**, 2714–2722 (2011).
31. Gaston, K. J., Davies, T. W., Bennie, J. & Hopkins, J. Reducing the ecological consequences of night-time light pollution: options and developments. *J. Appl. Ecol.* **49**, 1256–1266 (2012).
32. Greco, T. et al. How to impute study-specific standard deviations in meta-analyses of skewed continuous endpoints? *World J. Metaanal.* **3**, 215–224 (2015).
33. Altermatt, F. & Ebert, D. Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. *Biol. Lett.* **12**, 20160111 (2016).
34. Ayalon, I., de Barros Marangoni, L. F., Benichou, J. I. C., Avisar, D. & Levy, O. Red Sea corals under artificial light pollution at night (ALAN) undergo oxidative stress and photosynthetic impairment. *Glob. Change Biol.* **25**, 4194–4207 (2019).
35. Azam, C. et al. Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? *Glob. Change Biol.* **21**, 4333–4341 (2015).
36. Azam, C. et al. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landsc. Urban Plan.* **175**, 123–135 (2018).
37. Bailey, L. A., Brigham, R. M., Bohn, S. J., Boyles, J. G. & Smit, B. An experimental test of the allotonic frequency hypothesis to isolate the effects of light pollution on bat prey selection. *Oecologia* **190**, 367–374 (2019).
38. Baker, B. J. & Richardson, J. M. L. The effect of artificial light on male breeding-season behaviour in green frogs, *Rana clamitans melanota*. *Can. J. Zool.* **84**, 1528–1532 (2006).
39. Bedrosian, T. A., Aubrecht, T. G., Kaugars, K. E., Weil, Z. M. & Nelson, R. J. Artificial light at night alters delayed-type hypersensitivity reaction in response to acute stress in Siberian hamsters. *Brain Behav. Immun.* **34**, 39–42 (2013).
40. Bedrosian, T. A., Fonken, L. K., Walton, J. C. & Nelson, R. J. Chronic exposure to dim light at night suppresses immune responses in Siberian hamsters. *Biol. Lett.* **7**, 468–471 (2011).
41. Bennie, J., Davies, T. W., Cruse, D., Bell, F. & Gaston, K. J. Artificial light at night alters grassland vegetation species composition and phenology. *J. Appl. Ecol.* **55**, 442–450 (2018).
42. Bennie, J., Davies, T. W., Cruse, D., Inger, R. & Gaston, K. J. Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. *Phil. Trans. R. Soc. B* **370**, 20140131 (2015).
43. Bennie, J., Davies, T. W., Cruse, D., Inger, R. & Gaston, K. J. Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *J. Appl. Ecol.* **55**, 2698–2706 (2018).
44. Berry, M., Booth, D. T. & Limpus, C. J. Artificial lighting and disrupted sea-finding behaviour in hatchling loggerhead turtles (*Caretta caretta*) on the Woongarra coast, south-east Queensland, Australia. *Aust. J. Zool.* **61**, 137–145 (2013).
45. Bird, B. L., Branch, L. C. & Miller, D. L. Effects of coastal lighting on foraging behavior of beach mice. *Conserv. Biol.* **18**, 1435–1439 (2004).
46. Bliss-Ketchum, L. L., de Rivera, C. E., Turner, B. C. & Weisbaum, D. M. The effect of artificial light on wildlife use of a passage structure. *Biol. Conserv.* **199**, 25–28 (2016).
47. Brüning, A., Hölker, F., Franke, S., Preuer, T. & Kloas, W. Spotlight on fish: Light pollution affects circadian rhythms of European perch but does not cause stress. *Sci. Total Environ.* **511**, 516–522 (2015).
48. Brüning, A., Kloas, W., Preuer, T. & Hölker, F. Influence of artificially induced light pollution on the hormone system of two common fish species, perch and roach, in a rural habitat. *Conserv. Physiol.* **6**, coy016 (2018).
49. Carazo, I., Norambuena, F., Oliveira, C., Sánchez-Vázquez, F. J. & Duncan, N. J. The effect of night illumination, red and infrared light, on locomotor activity, behaviour and melatonin of Senegalese sole (*Solea senegalensis*) broodstock. *Physiol. Behav.* **118**, 201–207 (2013).
50. Cianchetti-Benedetti, M., Becciu, P., Massa, B. & Dell'Omo, G. Conflicts between touristic recreational activities and breeding shearwaters: short-term effect of artificial light and sound on chick weight. *Eur. J. Wildl. Res.* **64**, 19 (2018).
51. Cleary-Gaffney, M. & Coogan, A. N. Limited evidence for affective and diurnal rhythm responses to dim light-at-night in male and female C57Bl/6 mice. *Physiol. Behav.* **189**, 78–85 (2018).
52. Costin, K. J. & Boulton, A. M. A field experiment on the effect of introduced light pollution on fireflies (Coleoptera: Lampyridae) in the Piedmont Region of Maryland. *Coleopt. Bull.* **70**, 84–86 (2016).
53. Cravens, Z. M., Brown, V. A., Divoll, T. J. & Boyles, J. G. Illuminating prey selection in an insectivorous bat community exposed to artificial light at night. *J. Appl. Ecol.* **55**, 705–713 (2018).
54. Czarnecka, M., Kakareko, T., Jermacz, L., Pawlak, R. & Kobak, J. Combined effects of nocturnal exposure to artificial light and habitat complexity on fish foraging. *Sci. Total Environ.* **684**, 14–22 (2019).
55. Da Silva, A., Diez-Méndez, D. & Kempnaers, B. Effects of experimental night lighting on the daily timing of winter foraging in common European songbirds. *J. Avian Biol.* **48**, 862–871 (2017).
56. Da Silva, A. & Kempnaers, B. Singing from north to south: latitudinal variation in timing of dawn singing under natural and artificial light conditions. *J. Anim. Ecol.* **86**, 1286–1297 (2017).
57. Da Silva, A., Samplonius, J. M., Schlicht, E., Valcu, M. & Kempnaers, B. Artificial night lighting rather than traffic noise affects the daily timing of dawn and dusk singing in common European songbirds. *Behav. Ecol.* **25**, 1037–1047 (2014).
58. Da Silva, A., Valcu, M. & Kempnaers, B. Behavioural plasticity in the onset of dawn song under intermittent experimental night lighting. *Anim. Behav.* **117**, 155–165 (2016).
59. Dauchy, R. T. et al. Eliminating animal facility light-at-night contamination and its effect on circadian regulation of rodent physiology, tumor growth, and metabolism: a challenge in the relocation of a cancer research laboratory. *J. Am. Assoc. Lab. Anim. Sci.* **50**, 326–336 (2011).
60. Davies, T. W. et al. Multiple night-time light-emitting diode lighting strategies impact grassland invertebrate assemblages. *Glob. Change Biol.* **23**, 2641–2648 (2017).
61. Davies, T. W., Bennie, J. & Gaston, K. J. Street lighting changes the composition of invertebrate communities. *Biol. Lett.* **8**, 764–767 (2012).
62. Davies, T. W., Coleman, M., Griffith, K. M. & Jenkins, S. R. Night-time lighting alters the composition of marine epifaunal communities. *Biol. Lett.* **11**, 20150080 (2015).
63. de Jong, M. et al. Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species. *Phil. Trans. R. Soc. B* **370**, 20140128 (2015).
64. de Jong, M. et al. Dose-dependent responses of avian daily rhythms to artificial light at night. *Physiol. Behav.* **155**, 172–179 (2016).
65. De Medeiros, B. A. S., Barghini, A. & Vanin, S. A. Streetlights attract a broad array of beetle species. *Rev. Bras. Entomol.* **61**, 74–79 (2017).
66. Dimitriadis, C., Fournari-Konstantinidou, I., Sourbès, L., Koutsoubas, D. & Mazaris, A. D. Reduction of sea turtle population recruitment caused by nightlight: evidence from the Mediterranean region. *Ocean Coast. Manag.* **153**, 108–115 (2018).

67. Dominoni, D. M. et al. Dose-response effects of light at night on the reproductive physiology of great tits (*Parus major*): integrating morphological analyses with candidate gene expression. *J. Exp. Zool. A Ecol. Integr. Physiol.* **329**, 473–487 (2018).
68. Dominoni, D. M., Goymann, W., Helm, B. & Partecke, J. Urban-like night illumination reduces melatonin release in European blackbirds (*Turdus merula*): implications of city life for biological time-keeping of songbirds. *Front. Zool.* **10**, 60 (2013).
69. Dominoni, D. M., Helm, B., Lehmann, M., Dowse, H. B. & Partecke, J. Clocks for the city: circadian differences between forest and city songbirds. *Proc. Biol. Sci.* **280**, 20130593 (2013).
70. Dominoni, D. M., Quetting, M. & Partecke, J. Long-term effects of chronic light pollution on seasonal functions of European blackbirds (*Turdus merula*). *PLoS ONE* **8**, e85069 (2013).
71. Dong, Y. N., Goguen, D., Robertson, H. A. & Rusak, B. Anatomical and temporal differences in the regulation of ZIF268 (NGFI-A) protein in the hamster and mouse suprachiasmatic nucleus. *Abstr. Soc. Neurosci.* **111**, 567–574 (2002).
72. Durrant, J., Botha, L. M., Green, M. P. & Jones, T. M. Artificial light at night prolongs juvenile development time in the black field cricket, *Teleogryllus commodus*. *J. Exp. Zool. B Mol. Dev. Evol.* **330**, 225–233 (2018).
73. Durrant, J., Green, M. P. & Jones, T. M. Dim artificial light at night reduces the cellular immune response of the black field cricket, *Teleogryllus commodus*. *Insect Sci.* **27**, 571–582 (2020).
74. Firebaugh, A. & Haynes, K. J. Light pollution may create demographic traps for nocturnal insects. *Basic Appl. Ecol.* **34**, 118–125 (2019).
75. Flowers, N. D. & Gibson, D. J. Quantified effects of artificial versus natural nighttime lighting on the Eurasian grasses *Bothriochloa bladhii* (Poaceae) and *Bothriochloa ischaemum* (Poaceae) and the North American grasses *Panicum virgatum* (Poaceae) and *Sorghastrum nutans* (Poaceae). *J. Torrey Bot. Soc.* **145**, 147–155 (2018).
76. Fobert, E. K., da Silva, K. B. & Swearer, S. E. Artificial light at night causes reproductive failure in clownfish. *Biol. Lett.* **15**, 20190272 (2019).
77. Fonken, L. K., Haim, A. & Nelson, R. J. Dim light at night increases immune function in Nile grass rats, a diurnal rodent. *Chronobiol. Int.* **29**, 26–34 (2012).
78. Fonken, L. K., Kitsmiller, E., Smale, L. & Nelson, R. J. Dim nighttime light impairs cognition and provokes depressive-like responses in a diurnal rodent. *J. Biol. Rhythms* **27**, 319–327 (2012).
79. Fonken, L. K., Weil, Z. M. & Nelson, R. J. Mice exposed to dim light at night exaggerate inflammatory responses to lipopolysaccharide. *Brain Behav. Immun.* **34**, 159–163 (2013).
80. Foster, J. G., Algera, D. A., Brownscombe, J. W., Zolderdo, A. J. & Cooke, S. J. Consequences of different types of littoral zone light pollution on the parental care behaviour of a freshwater teleost fish. *Water Air Soil Pollut.* **227**, 404 (2016).
81. Francis, M. J., Spooner, P. & Matthews, A. The influence of urban encroachment on squirrel gliders (*Petaurus norfolcensis*): effects of road density, light and noise pollution. *Wildl. Res.* **42**, 324–333 (2015).
82. Frank, T. M., Gabbert, W. C., Chaves-Campos, J. & LaVal, R. K. Impact of artificial lights on foraging of insectivorous bats in a Costa Rican cloud forest. *J. Trop. Ecol.* **35**, 8–17 (2019).
83. Gastón, M. S., Pereyra, L. C. & Vaira, M. Artificial light at night and captivity induces differential effects on leukocyte profile, body condition, and erythrocyte size of a diurnal toad. *J. Exp. Zool. A Ecol. Integr. Physiol.* **331**, 93–102 (2019).
84. Grenis, K. & Murphy, S. M. Direct and indirect effects of light pollution on the performance of an herbivorous insect. *Insect Sci.* **26**, 770–776 (2019).
85. Grenis, K., Tjossem, B. & Murphy, S. M. Predation of larval Lepidoptera in habitat fragments varies spatially and temporally but is not affected by light pollution. *J. Insect Conserv.* **19**, 559–566 (2015).
86. Grubisic, M. et al. Artificial light at night decreases biomass and alters community composition of benthic primary producers in a sub-alpine stream. *Limnol. Oceanogr.* **62**, 2799–2810 (2017).
87. Grubisic, M., van Grunsven, R. H. A., Manfrin, A., Monaghan, M. T. & Hölker, F. A transition to white LED increases ecological impacts of nocturnal illumination on aquatic primary producers in a lowland agricultural drainage ditch. *Environ. Pollut.* **240**, 630–638 (2018).
88. Grunst, M. L., Raap, T., Grunst, A. S., Pinxten, R. & Eens, M. Artificial light at night does not affect telomere shortening in a developing free-living songbird: a field experiment: artificial light at night and telomere dynamics. *Sci. Total Environ.* **662**, 266–275 (2019).
89. Henn, M., Nichols, H., Zhang, Y. & Bonner, T. H. Effect of artificial light on the drift of aquatic insects in urban central Texas streams. *J. Freshw. Ecol.* **29**, 307–318 (2014).
90. Hoffmann, J., Palme, R. & Eccard, J. A. Long-term dim light during nighttime changes activity patterns and space use in experimental small mammal populations. *Environ. Pollut.* **238**, 844–851 (2018).
91. Hoffmann, J., Schirmer, A. & Eccard, J. A. Light pollution affects space use and interaction of two small mammal species irrespective of personality. *BMC Ecol.* **19**, 26 (2019).
92. Hölker, F. et al. Microbial diversity and community respiration in freshwater sediments influenced by artificial light at night. *Phil. Trans. R. Soc. B* **370**, 20140130 (2015).
93. Kempenaers, B., Borgström, P., Loës, P., Schlicht, E. & Valcu, M. Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr. Biol.* **20**, 1735–1739 (2010).
94. Kumar, J., Malik, S., Bhardwaj, S. K. & Rani, S. Bright light at night alters the perception of daylength in Indian weaver bird (*Ploceus philippinus*). *J. Exp. Zool. A Ecol. Integr. Physiol.* **329**, 488–496 (2018).
95. Le Tallec, T., Théry, M. & Perret, M. Melatonin concentrations and timing of seasonal reproduction in male mouse lemurs (*Microcebus murinus*) exposed to light pollution. *J. Mammal.* **97**, 753–760 (2016).
96. Lewanzik, D. & Voigt, C. C. Artificial light puts ecosystem services of frugivorous bats at risk. *J. Appl. Ecol.* **51**, 388–394 (2014).
97. Linley, G. D. The impact of artificial lighting on bats along native coastal vegetation. *Aust. Mammal.* **39**, 178–184 (2018).
98. Luarte, T. et al. Light pollution reduces activity, food consumption and growth rates in a sandy beach invertebrate. *Environ. Pollut.* **218**, 1147–1153 (2016).
99. Macgregor, C. J., Evans, D. M., Fox, R. & Pocock, M. J. O. The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. *Glob. Change Biol.* **23**, 697–707 (2017).
100. Macgregor, C. J., Pocock, M. J. O., Fox, R. & Evans, D. M. Effects of street lighting technologies on the success and quality of pollination in a nocturnally pollinated plant. *Ecosphere* **10**, e02550 (2019).
101. Manfrin, A. et al. Dietary changes in predators and scavengers in a nocturnally illuminated riparian ecosystem. *Oikos* **127**, 960–969 (2018).
102. McLay, L. K., Green, M. P. & Jones, T. M. Chronic exposure to dim artificial light at night decreases fecundity and adult survival in *Drosophila melanogaster*. *J. Insect Physiol.* **100**, 15–20 (2017).
103. McLay, L. K., Nagarajan-Radha, V., Green, M. P. & Jones, T. M. Dim artificial light at night affects mating, reproductive output, and reactive oxygen species in *Drosophila melanogaster*. *J. Exp. Zool. A Ecol. Integr. Physiol.* **329**, 419–428 (2018).
104. McMahon, T. A., Rohr, J. R. & Bernal, X. E. Light and noise pollution interact to disrupt interspecific interactions. *Ecology* **98**, 1290–1299 (2017).
105. Miller, C. R. et al. Combined effects of night warming and light pollution on predator–prey interactions. *Proc. Biol. Sci.* **284**, 20171195 (2017).
106. Miller, M. W. Apparent effects of light pollution on singing behavior of American robins. *Condor* **108**, 130–139 (2006).
107. Minnaar, C., Boyles, J. G., Minnaar, I. A., Sole, C. L. & McKechnie, A. E. Stacking the odds: light pollution may shift the balance in an ancient predator–prey arms race. *J. Appl. Ecol.* **52**, 552–531 (2015).
108. Moore, A. F. & Menaker, M. The effect of light on melatonin secretion in the cultured pineal glands of *Anolis* lizards. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **160**, 301–308 (2011).
109. Navarro-Barranco, C. & Hughes, L. E. Effects of light pollution on the emergent fauna of shallow marine ecosystems: amphipods as a case study. *Mar. Pollut. Bull.* **94**, 235–240 (2015).
110. Owens, A. C. S., Meyer-Rochow, V. B. & Yang, E. C. Short- and mid-wavelength artificial light influences the flash signals of *Aquatica ficta* fireflies (Coleoptera: Lampyridae). *PLoS ONE* **13**, e0191576 (2018).
111. Pendoley, K. & Kamrowski, R. L. Sea-finding in marine turtle hatchlings: what is an appropriate exclusion zone to limit disruptive impacts of industrial light at night? *J. Nat. Conserv.* **30**, 1–11 (2016).
112. Perkin, E. K., Hölker, F., Tockner, K. & Richardson, J. S. Artificial light as a disturbance to light-naïve streams. *Freshw. Biol.* **59**, 2235–2244 (2014).
113. Polak, T., Korine, C., Yair, S. & Holderied, M. W. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. *J. Zool.* **285**, 21–27 (2011).
114. Pulgar, J. et al. Endogenous cycles, activity patterns and energy expenditure of an intertidal fish is modified by artificial light pollution at night (ALAN). *Environ. Pollut.* **244**, 361–366 (2019).
115. Raap, T. et al. Artificial light at night affects body mass but not oxidative status in free-living nestling songbirds: an experimental study. *Sci. Rep.* **6**, 35626 (2016).
116. Raap, T., Casasole, G., Pinxten, R. & Eens, M. Early life exposure to artificial light at night affects the physiological condition: an experimental study on the ecophysiology of free-living nestling songbirds. *Environ. Pollut.* **218**, 909–914 (2016).
117. Raap, T., Sun, J., Pinxten, R. & Eens, M. Disruptive effects of light pollution on sleep in free-living birds: season and/or light intensity-dependent? *Behav. Processes* **144**, 13–19 (2017).
118. Rapatsa, M. M. & Moyo, N. A. G. The potential role of night-time lighting in attracting terrestrial insects as food for *Oreochromis mossambicus* and *Clarias gariepinus*. *Trop. Zool.* **30**, 156–169 (2017).

119. Reiter, R. J. et al. The pineal melatonin rhythm and its regulation by light in a subterranean rodent, the valley pocket gopher (*Thomomys bottae*). *J. Pineal Res.* **16**, 145–153 (1994).
120. Robert, K. A., Lesku, J. A., Partecke, J. & Chambers, B. Artificial light at night desynchronizes strictly seasonal reproduction in a wild mammal. *Proc. Biol. Sci.* **282**, 20151745 (2015).
121. Robertson, K., Booth, D. T. & Limpus, C. J. An assessment of 'turtle-friendly' lights on the sea-finding behaviour of loggerhead turtle hatchlings (*Caretta caretta*). *Wildl. Res.* **43**, 27–37 (2016).
122. Rotics, S., Dayan, T. & Kronfeld-Schor, N. Effect of artificial night lighting on temporally partitioned spiny mice. *J. Mammal.* **92**, 159–168 (2011).
123. Russo, D. et al. Adverse effects of artificial illumination on bat drinking activity. *Anim. Conserv.* **20**, 492–501 (2017).
124. Rydell, J., Eklöf, J. & Sánchez-Navarro, S. Age of enlightenment: long-term effects of outdoor aesthetic lights on bats in churches. *R. Soc. Open Sci.* **4**, 161077 (2017).
125. Sanders, D. et al. Artificial nighttime light changes aphid-parasitoid population dynamics. *Sci. Rep.* **5**, 15232 (2015).
126. Santos, C. D. et al. Effects of artificial illumination on the nocturnal foraging of waders. *Acta Oecol.* **36**, 166–172 (2010).
127. Schoech, S. J. et al. The effects of low levels of light at night upon the endocrine physiology of western scrub-jays (*Aphelocoma californica*). *J. Exp. Zool. A Ecol. Genet. Physiol.* **319**, 527–538 (2013).
128. Schoeman, M. C. Light pollution at stadiums favors urban exploiter bats. *Anim. Conserv.* **19**, 120–130 (2016).
129. Silva, E. et al. Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *J. Photochem. Photobiol. B* **173**, 240–249 (2017).
130. Simões, T. N., da Silva, A. C. & Carneiro de Melo Moura, C. Influence of artificial lights on the orientation of hatchlings of *Eretmochelys imbricata* in Pernambuco, Brazil. *Zoologia (Curitiba)* **34**, e13727 (2017).
131. Spoelstra, K., Ramakers, J. J. C., van Dis, N. E. & Visser, M. E. No effect of artificial light of different colors on commuting Daubenton's bats (*Myotis daubentonii*) in a choice experiment. *J. Exp. Zool. A Ecol. Integr. Physiol.* **329**, 506–510 (2018).
132. Spoelstra, K. et al. Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proc. Biol. Sci.* **284**, 20170075 (2017).
133. Sun, J., Raap, T., Pinxten, R. & Eens, M. Artificial light at night affects sleep behaviour differently in two closely related songbird species. *Environ. Pollut.* **231**, 882–889 (2017).
134. Szekeres, P. et al. Does coastal light pollution alter the nocturnal behavior and blood physiology of juvenile bonefish (*Albula vulpes*)? *Bull. Mar. Sci.* **93**, 491–505 (2017).
135. Talanda, J., Maszczyk, P. & Babkiewicz, E. The reaction distance of a planktivorous fish (*Scardinius erythrophthalmus*) and the evasiveness of its prey (*Daphnia pulex* × *pulicaria*) under different artificial light spectra. *Limnology* **19**, 311–319 (2018).
136. Taufique, S. K. T., Prabhat, A. & Kumar, V. Illuminated night alters hippocampal gene expressions and induces depressive-like responses in diurnal corvids. *Eur. J. Neurosci.* **48**, 3005–3018 (2018).
137. Thomas, J. R. et al. The impact of streetlights on an aquatic invasive species: artificial light at night alters signal crayfish behaviour. *Appl. Anim. Behav. Sci.* **176**, 143–149 (2016).
138. Ulgezen, Z. N. et al. The preference and costs of sleeping under light at night in forest and urban great tits. *Proc. Biol. Sci.* **286**, 20190872 (2019).
139. Underwood, C. N., Davies, T. W. & Queirós, A. M. Artificial light at night alters trophic interactions of intertidal invertebrates. *J. Anim. Ecol.* **86**, 781–789 (2017).
140. van Geffen, K. G. et al. Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecol. Entomol.* **40**, 401–408 (2015).
141. van Geffen, K. G. et al. Artificial light at night inhibits mating in a Geometrid moth. *Insect Conserv. Divers.* **8**, 282–287 (2015).
142. van Langevelde, F., van Grunsven, R. H. A., Veenendaal, E. M. & Fijen, T. P. M. Artificial night lighting inhibits feeding in moths. *Biol. Lett.* **13**, 20160874 (2017).
143. Vollrath, L. & Huesgen, A. Response of pineal serotonin N-acetyltransferase activity in male guinea pigs exposed to light pulses at night. *J. Neural Transm.* **72**, 55–66 (1988).
144. Wakefield, A., Broyles, M., Stone, E. L., Harris, S. & Jones, G. Quantifying the attractiveness of broad-spectrum street lights to aerial nocturnal insects. *J. Appl. Ecol.* **55**, 714–722 (2018).
145. Wang, W. et al. Effects of supplemental lighting with different light qualities on growth and secondary metabolite content of *Anoectochilus roxburghii*. *PeerJ.* **6**, e5274 (2018).
146. Watson, M. J., Wilson, D. R. & Mennill, D. J. Anthropogenic light is associated with increased vocal activity by nocturnally migrating birds. *Condor* **118**, 338–344 (2016).
147. Willmott, N. J., Henneken, J., Elgar, M. A. & Jones, T. M. Guiding lights: foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night. *Ethology* **125**, 289–287 (2019).
148. Willmott, N. J., Henneken, J., Selleck, C. J. & Jones, T. M. Artificial light at night alters life history in a nocturnal orb-web spider. *PeerJ.* **6**, e5599 (2018).
149. Yuen, S. W. & Bonebrake, T. C. Artificial night light alters nocturnal prey interception outcomes for morphologically variable spiders. *PeerJ.* **5**, e4070 (2017).
150. Zeale, M. R. K. et al. Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats. *Glob. Change Biol.* **24**, 5909–5918 (2018).
151. Zhang, S., Chen, X., Zhang, J. & Li, H. Differences in the reproductive hormone rhythm of tree sparrows (*Passer montanus*) from urban and rural sites in Beijing: the effect of anthropogenic light sources. *Gen. Comp. Endocrinol.* **206**, 24–29 (2014).
152. R Core Team R: *A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2018).
153. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48 (2010).
154. Hadfield, J. D. & Nakagawa, S. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J. Evol. Biol.* **23**, 494–508 (2010).
155. Rothstein, H. R., Sutton, A. J. & Borenstein, M. Publication Bias in Meta-Analysis: Prevention, Assessment and Adjustments (John Wiley & Sons, 2006).
156. Simonsohn, U., Nelson, L. D. & Simmons, J. P. P-curve: a key to the file-drawer. *J. Exp. Psychol. Gen.* **143**, 534–547 (2014).
157. Nakagawa, S. & Santos, E. S. A. Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* **26**, 1253–1274 (2012).
158. Simonsohn, U., Nelson, L. D. & Simmons, J. P. P-curve and effect size: correcting for publication bias using only significant results. *Perspect. Psychol. Sci.* **9**, 666–681 (2014).
159. Harrer, M., Cuijpers, P., Furukawa, T. & Ebert, D. D. Dmetar: Companion R Package for the Guide 'Doing Meta-Analysis in R'; <http://dmetar.protectlab.org>
160. Sanders, D., Frago, E., Kehoe, R., Patterson, C. & Gaston, K. J. A. *A Meta-Analysis of Biological Impacts of Artificial Light at Night*, v.4, Dryad, Dataset (Dryad, 2020); <https://doi.org/10.5061/dryad.wpzgmsbjn>

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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

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Reporting Summary

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Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

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/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research [guidelines for submitting code & software](#) for further information.

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Data availability

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

Field-specific reporting

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Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

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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 communit") 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	<i>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</i>
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 work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

Reporting for 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.

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<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

Methods

n/a	Involved in the study
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