

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

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12 **One sentence summary:** A meta-analysis of 126 published studies shows that exposure to artificial
13 light at night induced strong responses for physiological measures, daily activity patterns and life-
14 history traits.

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23 **Natural light cycles are being eroded over large areas of the globe by the direct emissions and**
24 **the sky brightening that result from sources of artificial nighttime light. This is predicted to**
25 **affect wild organisms, particularly because of the central role that light regimes play in**
26 **determining the timing of biological activity. Although numerous empirical studies have**
27 **reported such effects, these have focussed on particular species or local communities and have**
28 **thus been unable to provide a general evaluation of the overall frequency and strength of**
29 **these impacts. Using a new database of published studies, we show that exposure to artificial**
30 **light at night induces strong responses for physiological measures, daily activity patterns and**
31 **life-history traits. We found particularly strong responses for hormone levels, the onset of**
32 **daily activity in diurnal species, and life-history traits such as offspring number, predation,**
33 **cognition and sea-finding (in turtles). There have been few studies so far on the impact of**
34 **artificial light at night on ecosystem functions. The breadth and often strength of biological**
35 **impacts we reveal highlights the need for outdoor artificial nighttime lighting to be limited to**
36 **the places and forms (such as timing, intensity, spectrum) in which it is genuinely required by**
37 **the people using it to minimise ecological impacts.**

38

39 The development of electric lighting technology has transformed human societies, lengthening the
40 available time both for work and pleasure¹. Associated with human settlement, transport networks
41 and industry, it has also profoundly altered the natural nighttime environment. Large areas of the
42 Earth now experience light that differs from natural regimes in timing, intensity and spectrum^{2,3}.
43 Nearly a quarter of the global land area already lies under artificially light-polluted nighttime skies⁴.
44 The area experiencing direct emissions from artificial light sources is estimated currently to be
45 expanding at c.2% per annum, with localities that were previously lit brightening further at a similar
46 rate⁵.

47

48 Artificial light at night (ALAN) is predicted to constitute a significant anthropogenic pressure on
49 natural biological systems because (i) such systems are organised foremost by light, and particularly
50 by daily and seasonal cycles of light and dark⁶⁻⁸, and (ii) there have been no natural analogues, at
51 any timescale, to the form, extent, distribution, timing or rate of spread of artificial lighting³. More
52 obvious impacts like delayed retention of leaves on trees close to streetlights and attraction of
53 insects and birds to outdoor lights, have long been documented⁹⁻¹¹. However, particularly the last
54 decade has seen rapid growth in the numbers of empirical studies testing for impacts of ALAN on a
55 broad array of biological phenomena across a wide diversity of organisms (e.g. ¹²⁻¹⁶). Although
56 there have been qualitative reviews of this literature^{2,17,18}, quantitative analyses and understanding
57 of the frequency and strength of biological impacts of ALAN are lacking.

58

59 Here we report the results of a meta-analysis, which takes into account the hierarchical structure of
60 data due to non-independence of several outcomes coming from the same study^{19,20}, to build a
61 quantitative understanding of the biological impacts of ALAN on a variety of responses from
62 organisms and ecological communities. Following a systematic search, we identified 126
63 publications from the peer-reviewed literature testing for the impact of ALAN on organisms. Each
64 individual measure was assigned to one of five major response categories: physiology, seasonal
65 phenology, life-history traits, daily activity patterns, and population/community. The entire data set
66 covered a wide range of different measurements for each of the five categories and of different
67 study organisms and habitats, and included field and laboratory studies.

68

69 **Results and Discussion**

70 Overall, the dataset was dominated by physiological, life-history trait and population/community-
71 based measures, ranging from strong negative to strong positive responses to ALAN exposure (Fig.
72 1). Thirty-five studies documented 338 observations reporting the impact on organismal
73 physiology, seven studies yielded 35 observations reporting the impact on organismal phenology,

74 58 studies reported 411 life-history measures, 27 studies described 139 daily activity measures, and
75 42 studies gave 381 observations of the impact on populations and ecological communities. We
76 organised these measures into subcategories within each of the five main response categories (see
77 Methods and Fig. 2). This led to the exclusion of 196 measures from the analysis of subcategories
78 because these were only included if they had measures from at least five different studies.

79

80 Of the physiological measures, effect sizes for hormone levels (mostly melatonin) indicated that
81 these were consistently and markedly reduced across all studies included (Fig. 2). By contrast, gene
82 expression varied markedly in effect sizes, including a number of very strong positive responses
83 (Fig. 2a). The impact on these two measures is important as this can have knock-on effects on other
84 physiological parameters such as health and alertness. The other three physiological measures
85 (immune and stress responses and glands/structures) did not show an overall response to ALAN,
86 however the frequency distributions of effect sizes for immune and stress responses (Fig. 2c,d,e)
87 show that this does not mean that ALAN has no impact, but rather that depending on the conditions
88 of the study the response may be either positive or negative. For stress responses, the frequency
89 distribution of effect sizes appears bimodal, with peaks at low negative and higher positive values
90 (Fig. 2d).

91

92 While single studies find evidence of phenological shifts in plants under ALAN exposure²¹, our
93 dataset suggests that across plants and birds both positive and negative effect sizes for phenology
94 have been documented (Fig. 2f) with no evidence for an overall consistent directional shift.

95

96 Amongst measures of life-history traits (the term being used here broadly), overall measures of
97 cognition (mostly the performance of rodents in experimental tests) and offspring number were
98 negatively impacted by ALAN, and measures of predation were positively impacted (Fig. 2). Most
99 conspicuously, and including some high effect sizes, measures of sea-finding by young turtles (i.e.

100 the ability to find the right direction towards the sea) were regularly strongly impacted by ALAN
101 (Fig. 2n), reflecting movement towards the (landward) light source. This has significant
102 consequences for turtle survival, although the impact can to some degree be mitigated by careful
103 design, positioning and shielding of lights²².

104

105 ALAN impacts were particularly marked for daily activity patterns with, overall, the onset of
106 activity being pushed earlier and its cessation being delayed (Fig. 2). This did not manifest as an
107 overall strong effect of ALAN on the duration of diurnal or nocturnal activity, however in both
108 cases the impacts were very varied and included strong positive and negative effect sizes (Fig.
109 2p,q). This highlights the diversity of influences of ALAN on different species, increasing the
110 duration of activity of some while reducing it for others^{23,24}, and acting as an attractor for some
111 while as a repellent for others²⁵. We looked in more detail at this directional variation for two
112 animal groups, rodents and birds, that have been disproportionately well studied. For rodents, the
113 duration of activity of both diurnal and nocturnal species tended to be reduced by exposure to
114 ALAN (Fig. 3a). In contrast, for birds - with all of those included strictly diurnal - ALAN was more
115 likely to lead to an extension of the duration of their activity, with onset and cessation of singing
116 and foraging showing especially marked responses. This can go further in some groups, such that
117 diurnal species can use the so-called “nighttime niche” to extend their activity into the nighttime¹⁵.

118

119 We found little evidence for a strong overall or net impact of ALAN on the abundance of species or
120 the diversity of communities (Fig. 2). This outcome could potentially be explained as a consequence
121 of the variation in, and possible trade-offs and synergies between, individual-level physiological,
122 phenology, life-history and activity responses. Indeed, abundance responses showed some of the
123 greatest variation in effect sizes, from strongly negative to strongly positive, of any measured
124 biological impacts of ALAN (Fig. 2r). For bats, for which the impacts of ALAN have attracted
125 disproportionate scientific and policy attention²⁶, activity (here used as a measure of the presence or

126 abundance of species, rather than of the timing of individual movements) did not show an overall
127 strong negative response (Fig. 2). However, whilst some effect sizes were positive there was also a
128 long tail of marked negative responses, highlighting that some bat species are strongly repelled by
129 artificial light (Fig. 2g). Such complex patterns of responses may be typical of many taxonomic
130 groups, with the overall response being driven by those species that are most dominant.

131

132 Species interactions are an important building block of ecological community structure. Predation,
133 the most frequently studied interaction, was typically increased by ALAN exposure (Fig. 2l),
134 indicating that interactions between species can be highly sensitive to ALAN and are key for
135 understanding of how whole communities are impacted (as shown in food webs¹⁵ and also
136 pollination networks¹³). This seems likely in turn to lead to impacts of ALAN on ecosystem
137 functions, but so far these have been little studied^{13,15} and could not therefore, be separately
138 addressed in this metanalysis.

139

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

146

147 Overall, for most variables we did not find evidence for publication bias in effect sizes, in particular
148 there was no evidence of p-hacking in any of the variables and no evidence of funnel plot
149 asymmetry for most of them (Supplementary Table 1 and Supplementary Fig. 1). There was some
150 statistical evidence for funnel plot asymmetry for hormone levels, sea-finding by turtles, and
151 activity on and offset (and also for gene expression, gland structure and bat activity, but these

152 showed no strong overall directional effect size; Supplementary Table 1 and Supplementary Fig. 1).
153 However, in all of these cases this asymmetry may be driven by the biological nature of these
154 responses rather than being the result of publication bias. For example, effect sizes for hormone
155 levels predominantly concern the suppression of melatonin levels by artificial light, with
156 overproduction being an unlikely outcome. Likewise, for sea-finding in turtles any diversion of
157 movement from the direction of the sea is negative for the individuals concerned and results in a
158 negative effect size, and any normal movement would be regarded as an absence of effect (rather
159 than a positive one).

160

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

176

177 Notwithstanding the widespread nature of the biological effects of ALAN demonstrated by the
178 results reported here, marked biases continue to exist in the taxonomic groups and regions for which
179 empirical studies of these effects have been conducted. Of the 1304 effect sizes included in the
180 meta-analysis, 24 were for microbial communities, 143 for plants, 388 for invertebrates and 746 for
181 vertebrates. The dataset includes almost double the number of field studies (82) as compared to
182 laboratory experiments (42), with the majority of field studies in the meta-analysis from Europe
183 (46), North America (17) and Australia (7). Tropical regions were markedly under-represented,
184 despite the prediction that effects of ALAN could be particularly strong at low latitudes because of
185 the limited natural seasonal variation in the lengths of daylight and nighttime⁶. Further, more
186 research is needed on the response of whole ecological communities and their functions to ALAN
187 exposure²⁹; the strong response of trophic behaviour to ALAN suggests that species interactions
188 change, and with them whole community structures and their functions will shift. Interactions with
189 other human pressures, especially climate change are of particular interest, as for species that
190 exploit the nighttime niche their behaviour at night is often temperature dependent.

191

192 **Conclusion**

193 The results reported here have significant implications for the much-discussed mitigation of the
194 effects of ALAN on the natural environment^{30,31}. First, they underline how widespread these effects
195 are, including on diurnal species, and that where possible mitigation should be routine rather than
196 limited to places and times when taxa perceived to be of particular concern (e.g. bats) are active.
197 Second, they highlight the challenge of making recommendations for regulation of the maximum
198 intensities of particular kinds of lighting, given that marked biological impacts of ALAN occur
199 across a wide range of intensities including very low lighting levels (below 1 lux). Third, we show
200 that ALAN especially changes the physiology and behaviour of organisms by affecting hormone
201 levels, onset of daily activity, feeding and phototaxis but typically with a less strong impact on
202 particular community responses such as abundance and species richness, and this suggests that the

203 impact on community structure and diversity might be less clear and depends on the impacts on key
204 players (species or groups²⁹). Although species richness was not systematically affected in our
205 study, it is possible that ALAN is often altering community composition (i.e. beta diversity) so that
206 sensitive species are being replaced.

207
208 Concern has repeatedly been expressed about the impacts of the loss of natural nighttime light
209 cycles on humans that span from their physiology to their psychological sense of place⁹. Here we
210 show that a broad array of marked impacts also occur on other organisms.

211

212 **METHODS**

213 **Literature search.** We identified relevant literature using keyword searches in Web of Science (we
214 used “All databases” including Web of Science Core Collection, BIOSIS Citation Index, KCI-
215 Korean Journal Database, MEDLINE, Russian Science Citation Index and SciELO Citation Index)
216 and Scopus, finding any available papers published until 22 October 2019 (we constrained our
217 searches to these databases to focus on peer-reviewed studies, and tested for publication bias – see
218 below). We used the terms: "TS= (("Artificial light* at night" OR "Light* pollution" OR "Light* at
219 night" OR "night time light*") AND ("species" OR "ecosystem*" OR "ecological commun") AND
220 ("abundance" OR "behaviour" OR "richness" OR “reproduction" OR "mating" OR "*diversity" OR
221 "composition" OR "predation" OR "herbivory" OR "activity" OR "timing" OR "physiology" OR
222 "flight to light*" OR "melatonin" OR "development" OR "trophic" OR "biomass" OR
223 "pollination"))". After removing 352 duplicates, combining the searches resulted in 614
224 publications that were screened for inclusion criteria. To be included in the meta-analysis, studies
225 needed to (1) test for ALAN effects on organisms either in the field or the lab; (2) have a control
226 group that was exposed to natural light levels at night (or a dark control) and treatment groups with
227 exposure to ALAN up to 100 lux - studies with higher levels were excluded as these are unlikely to
228 occur in the field; (3) have at least 2 replicates per treatment; and (4) contain data on means, an

229 estimation of variation and sample size. If only box plots were presented, we extracted the median
230 and interquartile range³². This resulted in 126 papers, with a total of 1304 effect size measures (refs
231 12,13,15,16,25,27,28,33-151).

232

233 **Effect size categorizing.** We categorised the effect size measures into five different main groups:
234 response to exposure to artificial light at night of (i) organismal physiology, (ii) phenology, (iii)
235 organismal life history traits, (iv) activity (e.g. daily diurnal, nocturnal activity), or (v) populations
236 and communities. For the analyses, we were interested in which factors drive the response within
237 each category. We selected subcategories within each of the five major categories that we think
238 describe the dataset best. For each subcategory to be included in the analysis it needed to have data
239 that were extracted from at least five different studies. Below we briefly explain the subcategories.

240

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

244

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

247

248 *Life history traits.* Life-history traits are traits that affect the life table of an organism and therefore
249 its fitness. Based on the biology of the different species studied, the different effect sizes have been
250 classified as either having a positive or negative relationship with fitness. To express the fitness
251 consequences of all effect sizes, effect sizes were multiplied by -1 when the relationship between
252 the trait and fitness was negative. Effect sizes larger than zero thus express a benefit for the
253 organism, whereas the opposite is true for values lower than zero. A total of six categories were

254 considered: Sea finding in turtles, Predation risk, Body size, Cognition, Feeding, Predation, and
255 Reproductive output.

256

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

279

280 *Activity*. The data for daily activity patterns contains measures of when animals started or ceased
281 their activity (mostly measured against sunrise and sunset) and the duration of their activity. This
282 resulted in four subcategories: activity cessation, activity onset, diurnal activity duration, nocturnal
283 activity duration. One study measured the time spend inactive, this was included in activity duration
284 by changing the sign of the effect size.

285

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

291

292 **Data analysis.** The meta-analysis was conducted in R version 3.6.0¹⁵² using the package metafor¹⁵³
293 to estimate the standardized mean difference (Hedges' d) and corresponding sampling variance for
294 each data point using the “escalc(measure= "SMDH")” command. These values were then used to
295 fit a meta-analytic model in MCMCglmm¹⁹. To achieve this, the random term idh(SE):units was
296 fixed to one in the prior so that all measurement errors could be considered as independent of each
297 other. In addition, to account for study level non-independence due to multiple measurements per
298 study, “Study” was included as a random effect. The MCMC chain ran for 150,000 iterations, and it
299 was sampled every 50 iterations with the first 50,000 removed as burn-in to prevent autocorrelation
300 among subsequent iterations. Autocorrelation between consecutive samples was always lower than
301 0.1, and convergence of the chains was inspected visually to ensure that there were no trends in the
302 chain and that posterior distributions were not skewed. Significance is reported as the pMCMC
303 statistic^{19,154}. As we did not have any a priori knowledge on the distribution of our data, we used a
304 flat prior: the inverse-Gamma prior ($V = 1$, $\nu = 0.002$). Hedges' d was used to compare measures
305 of the variables between treatment and control. We present the mean effect size and 95% credible

306 intervals; the mean effect size was considered significantly different from 0 if its 95% CI did not
307 include 0.

308

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

311

312 **Testing for publication bias.** For all variables in the meta-analysis we assessed evidence of
313 publication bias. Publication bias implies that studies with low effect sizes were less likely to be
314 published than studies with larger effect sizes¹⁵⁵. These assumptions, however, are not always valid
315 and some authors suggest that publication bias is mostly caused by significance levels and p-
316 hacking¹⁵⁶. The first form of bias was tested using asymmetry in funnel plots of meta-analytic
317 residuals against the inverse of their precision (defined as 1/sampling variance)¹⁵⁷. For multilevel
318 meta-analysis models, funnel plots based on meta-analytic residuals (the sum of effect-size-level
319 effects and sampling-variance effects) are better suited than those based on effect sizes¹⁵⁸. We
320 interpreted asymmetry in funnel plots carefully given the small sample sizes for some variables, and
321 the lack of bidirectional outcomes for light impact on some traits, which will inevitably lead to a
322 biased plot. For example, for turtles, if there is an impact of exposure to ALAN on seafinding this
323 will always be negative. Further, we ran Egger's regressions using the meta-analytic residuals as the
324 response variable, and precision as the moderator¹⁵⁸. If the intercept of the Egger's regression does
325 not overlap zero, estimates from the opposite direction to the meta-analytic mean might be missing
326 which can be evidence of publication bias¹⁵⁸. P-value hacking was tested with the p-curve
327 technique, which can provide evidence of p-hacking if values close to the significance level 0.05 are
328 overrepresented in the data^{156,159}. The p-curve was performed with the function pcurve from the
329 dmetar package¹⁶⁰.

330

331 **Data availability**

332 All data generated or analysed during this study are available from the Dryad Digital Repository¹⁶¹.

333

334 **Code availability**

335 The computer code for the meta-analysis is available from the Dryad Digital Repository¹⁶¹.

336

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769 **Author contributions**

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

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773 **Competing interests**

774 The authors declare no competing interests.

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

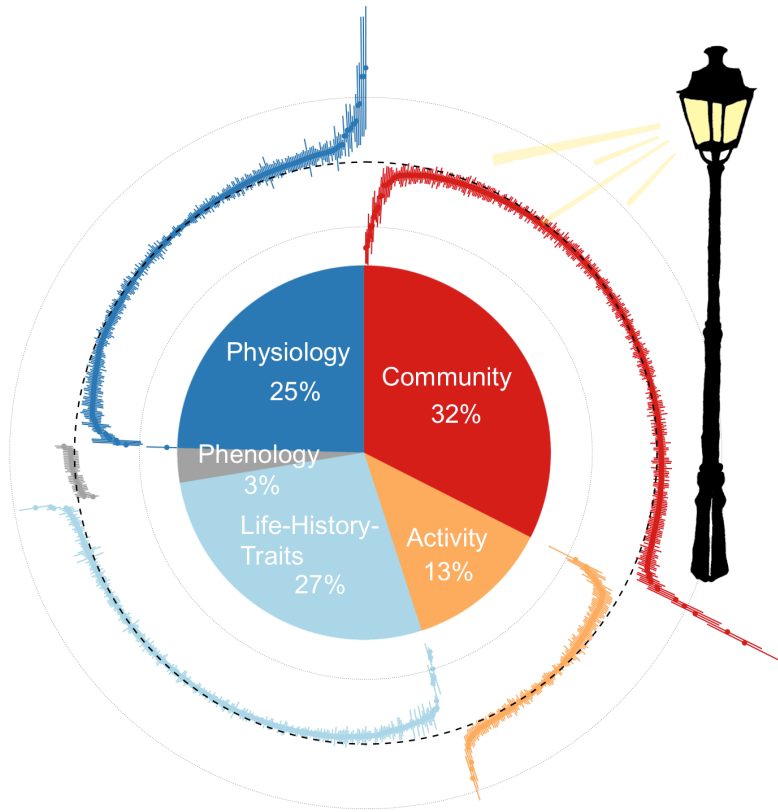
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785 **Figure 2. Effect sizes for the measures from the main categories.** Effect sizes (Hedges' d) with
786 post mean and 95% credible intervals based on results from MCMCglmm's for each variable from
787 the five main categories (physiology, phenology, life-history traits, activity, and
788 population/community). Numbers in brackets indicate the sample size and * the significance level
789 for pMCMC, with ***<0.001, **<0.01, *<0.05). Histograms a-t show the distribution of the effect
790 sizes for each of the categories, with the black dashed line indicating the zero x-axis intercept, the
791 range of effect size values on the x-axis and frequency on the y-axis.

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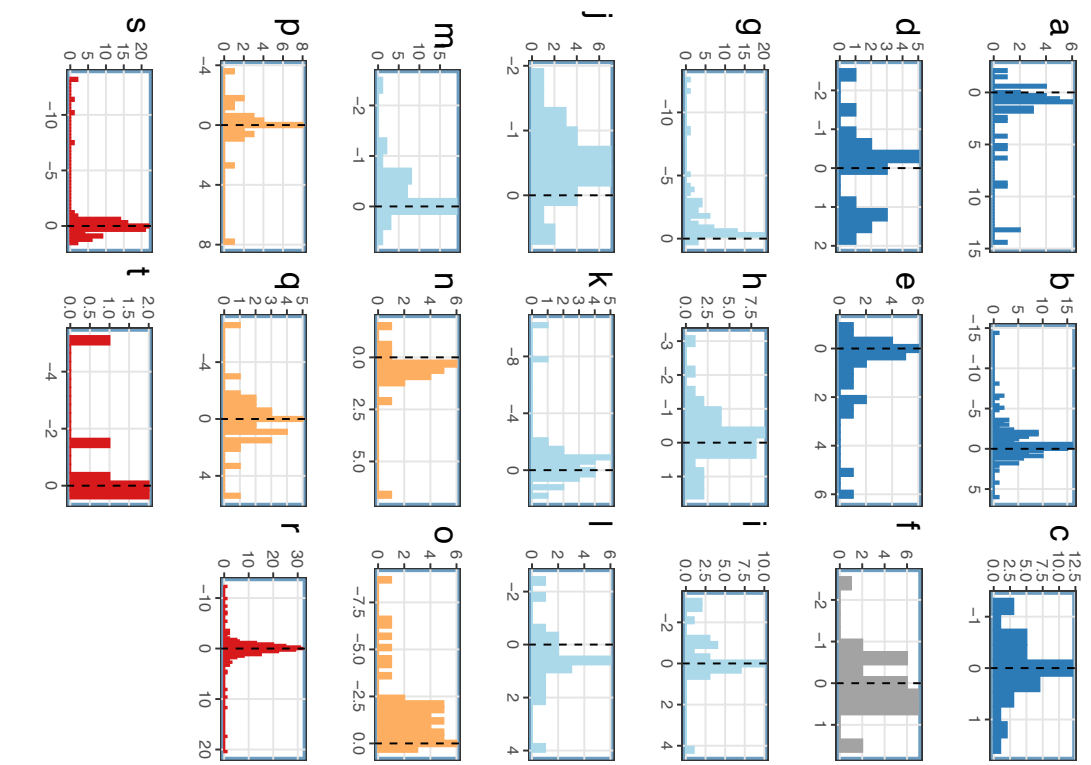
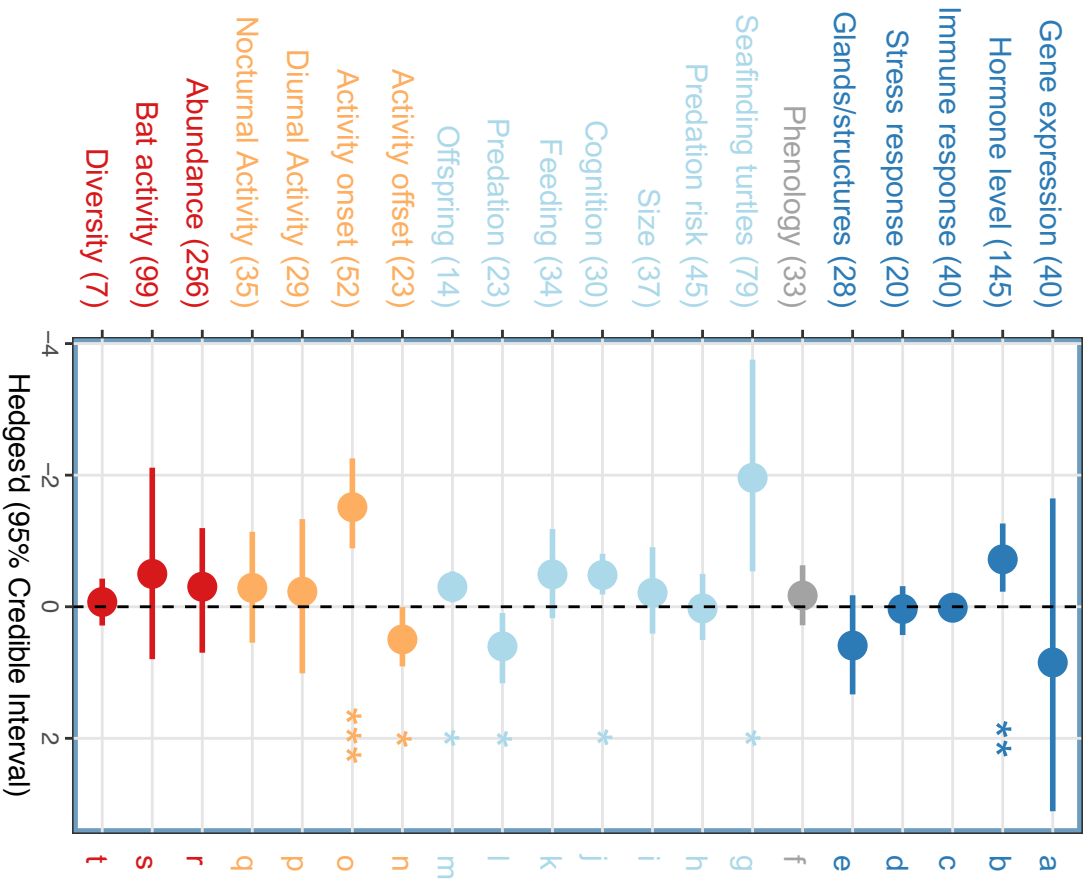
793 **Figure 3. Activity patterns and light intensity. (a)** Impact of ALAN on rodent and bird activity.
794 Effect sizes (Hedges' d) with post mean and 95% credible intervals based on results from
795 MCMCglmm's for each variable. **(b)** Impact of ALAN on diurnal and nocturnal species for the
796 categories: physiology, life-history traits and activity. **(c)** Meta regression of effect sizes and
797 artificial light intensity levels for organismal physiology (blue), phenology (grey), life-history traits
798 (light blue), activity (orange) and population/communities (red). Numbers in brackets indicate the
799 sample size and * the significance level for pMCMC, with ***<0.001, **<0.01, *<0.05, (*) <0.06).

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Community Activity Life History Traits Physiology



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