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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Natural light cycles are being eroded over large areas of the globe by the direct emissions and the sky brightening that result from sources of artificial nighttime 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 numerous empirical studies have reported such effects, these have focussed 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 for hormone levels, the onset of daily activity in diurnal species, and life-history traits such as offspring number, predation, cognition and sea-finding (in turtles). There have been few studies so far on the impact of artificial light at night on ecosystem functions. The breadth and often strength of biological impacts we reveal highlights the need for outdoor artificial nighttime lighting to be limited to the places and forms (such as timing, intensity, spectrum) in which it is genuinely required by the people using it to minimise ecological impacts.

The development of electric lighting technology has transformed human societies, lengthening the available time both for work and pleasure[1]. Associated with human settlement, transport networks and industry, it has also profoundly altered the natural nighttime 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 nighttime skies[4]. The area experiencing direct emissions from artificial light sources is estimated currently to be expanding at c.2% per annum, with localities that were previously lit brightening further at a similar rate[5].

Artificial light at night (ALAN) is predicted to constitute a significant anthropogenic pressure on natural biological systems because (i) such systems are organised foremost by light, and particularly by daily and seasonal cycles of light and dark[6-8], and (ii) there have been no natural analogues, at any timescale, to the form, extent, distribution, timing or rate of spread of artificial lighting[3]. 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 numbers of empirical studies testing for impacts of ALAN on a broad array of biological phenomena across a wide diversity of organisms (e.g. [12-16]). Although there have been qualitative reviews of this literature[2,17,18], quantitative analyses and understanding of the frequency and strength of biological impacts of ALAN are lacking.

Here we report the results of a meta-analysis, which takes into account the hierarchical structure of data due to 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. Following a systematic search, we identified 126 publications from the peer-reviewed literature testing for the impact of ALAN on organisms. Each individual measure was assigned to one of five major response categories: physiology, seasonal phenology, life-history traits, daily activity patterns, and population/community. The entire data set 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, seven 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 gave 381 observations of the impact on populations and ecological communities. We organised these measures into subcategories within each of the five main response categories (see 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 five different studies.

Of the physiological measures, effect sizes for hormone levels (mostly melatonin) indicated that these were consistently and markedly reduced across all studies included (Fig. 2). By contrast, gene expression varied markedly in effect sizes, including a number of very strong positive responses (Fig. 2a). The impact on these two measures is important as 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 for immune and stress responses (Fig. 2c,d,e) show that this does not mean that ALAN has no impact, but rather that depending on the conditions of the study the response may be either positive or negative. For stress responses, the frequency distribution of effect sizes appears bimodal, with peaks at low negative and higher positive values (Fig. 2d).

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

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

the ability to find the right direction towards the sea) were regularly strongly impacted by ALAN (Fig. 2n), reflecting movement towards the (landward) light source. This has significant consequences for turtle survival, although the impact can to some degree be mitigated by careful design, positioning and shielding of lights[22].

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. 2p,q). This highlights the diversity of influences of ALAN on different species, increasing the duration of activity of some while reducing it for others[23,24], and acting as an attractor for some while as a repellent for others[25]. We looked in more detail at this directional variation for two animal groups, rodents and birds, that 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 can go further in some groups, such that diurnal species can use the so-called "nighttime niche" to extend their activity into the nighttime[15].

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. 2r). For bats, for which the impacts of ALAN have attracted disproportionate scientific and policy attention[26], 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 webs[15] and also

136   pollination networks[13]). 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 ALAN[27], 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 nighttime[6]. Further, more

186 research is needed on the response of whole ecological communities and their functions to ALAN

187 exposure[29]; 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 groups[29]). 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 place[9]. 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 range[32]. 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 3.6.0[152] using the package metafor[153]

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 MCMCglmm[19]. 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 sizes[155]. These assumptions, however, are not always valid

315 and some authors suggest that publication bias is mostly caused by significance levels and p-

316 hacking[156]. 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 sizes[158]. 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 moderator[158]. 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 bias[158]. 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 package[160].

330

331 **Data availability**

332 All data generated or analysed during this study are available from the Dryad Digital Repository[161].

333

Code availability

335 The computer code for the meta-analysis is available from the Dryad Digital Repository[161].

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
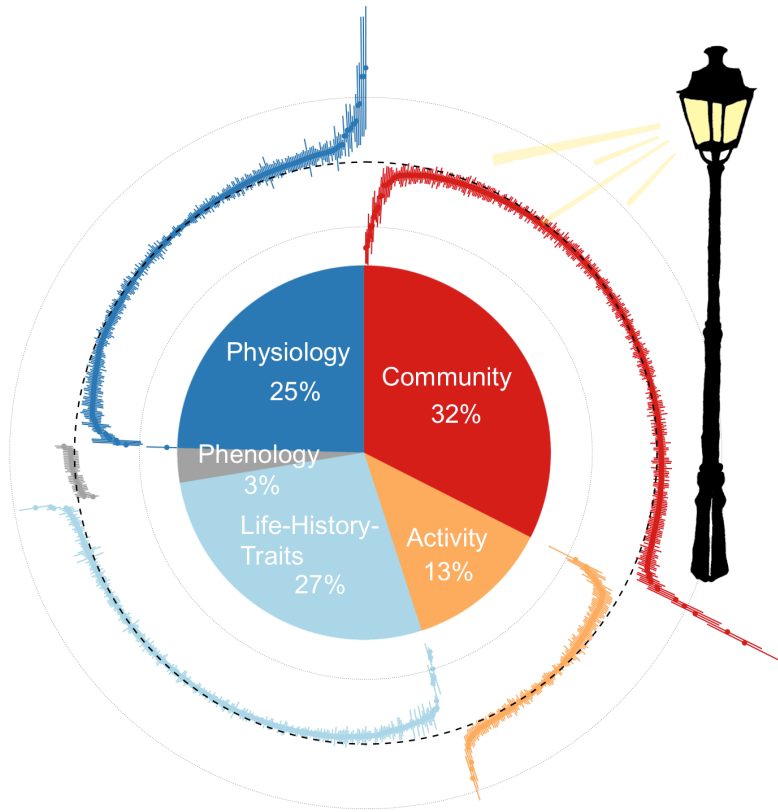783 measures belonging to each of the five categories.

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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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