Personality and artificial light at night in a semi-urban songbird population : no evidence for personality-dependent sampling bias, avoidance or disruptive effects on sleep behaviour

1 **Personality and artificial light at night in a semi-urban songbird population: no evidence**

2 **for personality-dependent sampling bias, avoidance or disruptive effects on sleep**

3 **behaviour**

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Abstract

Light pollution or artificial light at night (ALAN) is an increasing, worldwide challenge that affects many aspects of animal behaviour. Interestingly, the response to ALAN varies widely among individuals within a population and variation in personality (consistent individual differences in behaviour) may be an important factor explaining this variation. Consistent individual differences in exploration behaviour in particular may relate to the response to ALAN, as increasing evidence indicates its relation with how individuals respond to novelty and how they cope with anthropogenic modifications of the environment. Here, we assayed exploration behaviour in a novel environment as a proxy for personality variation in great tits (*Parus major*). We observed individual sleep behaviour over two consecutive nights, with birds sleeping under natural dark conditions the first night and confronted with ALAN inside the nest box on the second night, representing a modified and novel roosting environment. We examined whether roosting decisions when confronted with a camera (novel object), and subsequently with ALAN, were personality-dependent, as this could potentially create sampling bias. Finally, we assessed whether experimentally challenging individuals with ALAN induced personality-dependent changes in sleep behaviour.

Slow and fast explorers were equally likely to roost in a nest box when confronted with either a camera or artificial light inside, indicating the absence of personality-dependent sampling bias or avoidance of exposure to ALAN. Moreover, slow and fast explorers were equally disrupted in their sleep behaviour when challenged with ALAN. Whether other behavioural and physiological effects of ALAN are personality-dependent remains to be determined. Moreover, the sensitivity to disturbance of different behavioural types might depend on the behavioural context and the specific type of challenge in question. In our increasingly urbanized world, determining whether the effects of anthropogenic stressors

40 depend on personality type will be of paramount importance as it may affect population

41 dynamics.

42 CAPSULE: No evidence for personality-dependent responses to artificial light at night

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44 KEYWORDS: artificial light at night; exploration behaviour; sampling bias; sleep;

45 urbanization

Introduction

Urbanization presents organisms with a variety of novel and challenging situations, as human disturbance often drastically changes environments. These human-induced environmental changes include climate change, habitat loss and fragmentation, and the spread of exotic species (Wong and Candolin 2015). Moreover, increasing urbanization has led to a dramatic worldwide increase in artificial light at night (ALAN), or light pollution (Falchi et al. 2016). Light pollution impacts natural light dark cycles, posing a potential global threat for wildlife, biodiversity and humans (Davies and Smyth 2018). Increasing evidence shows disruptive effects of ALAN on animal physiology, such as changes in levels of melatonin, testosterone, and immune parameters, as well as animal behaviour (reviewed in Gaston et al. 2017). For instance, in songbirds ALAN affects the timing of singing behaviour, daily activity patterns, sleep behaviour, and breeding behaviour (see e.g. Kempenaers et al. 2010; Dominoni and Partecke 2015; Raap et al. 2015) .

Individuals of the same species and population may differ in how strongly they respond to environmental disturbances such as ALAN (Sih et al. 2012). For example, in blue tits (*Cyanistes caeruleus*), yearling males appeared to show a stronger response to ALAN than older individuals, as light pollution increased extra pair paternity rates more in yearling males than in older males (Kempenaers et al. 2010). Similarly, the disruptive effect of ALAN on sleep behaviour in great tits (*Parus major*) varied greatly among females during the nestling period (Raap et al. 2016b). When exposed to ALAN, some individuals seemed unaffected while others did not sleep at all. Moreover, about one in three great tits will no longer roost in a nest box with artificial light inside (Raap et al. 2017b).

Variation in personality may be an important factor explaining individual-level differences in behavioural responses to anthropogenic disturbance in general (Sih et al. 2012),

and ALAN in particular. Personality refers to individual differences in behaviour that are

consistent across time and/or context, and behavioural traits commonly found to be consistent

include aggressiveness, boldness and exploration behaviour (Reale et al. 2007). In the great tit,

novel environment exploration (henceforth exploration behaviour) is commonly used as a way

to operationalize exploratory personality (Verbeek et al. 1994; Dingemanse et al. 2002), as it is

heritable (Dingemanse et al. 2002; Quinn et al. 2009; Nicolaus et al. 2012) and repeatable in

several European populations (Dingemanse et al. 2012; Stuber et al. 2013), including in our

population (Thys et al. 2017). Individuals differ in how they explore a novel environment,

ranging from those that explore an area slowly but thoroughly (so-called slow explorers), to

those that explore rapidly but superficially (so-called fast explorers; Verbeek et al. 1994).

Exploration behaviour influences fitness (Dingemanse and Reale 2005) and covaries with other

personality traits, such as boldness (e.g. van Oers et al. 2004; Hollander et al. 2008) and

aggressiveness (Thys et al. 2017), as well as other ecologically relevant behaviours, including

dispersal tendency and foraging patterns (e.g. Dingemanse et al. 2003; van Overveld and

Matthysen 2010). Moreover, variation in exploration behaviour is linked to differences in stress

physiology, which affects how individuals cope with challenging situations (Carere et al. 2010;

Baugh et al. 2017), and likely influences patterns of behaviour in the urban matrix (Sih et al.

2012; Lowry et al. 2013).

Fast explorers are also more likely than slow explorers to accept and approach novel

objects (i.e. they are less neophobic), both in the laboratory (Verbeek et al. 1994; Carere et al.

2005; Baugh et al. 2017) and field (Stuber et al. 2013; Cole and Quinn 2014), and responses to

novelty may be particularly relevant when considering responses to anthropogenic

modifications of the environment (Tryjanowski et al. 2016), such as ALAN. For instance, fast

explorers were more likely than slow explorers to roost in the same nest box on subsequent

winter nights when a video camera (novel object) was installed inside (Stuber et al. 2013), and

breeding great tits with different personality types differed in their response to noise when feeding nestlings, with slow explorers taking longer to enter the nest box during noise playback than fast explorers (Naguib et al. 2013). Along this line, we previously demonstrated that about one in three birds do not roost in a nest box when confronted with a light inside, representing a modified and novel roosting environment, whereas birds always enter when the light is off (Raap et al. 2017b). Moreover, for those individuals that do roost in a nest box with light inside, ALAN caused disruptive effects on sleep behaviour, but interestingly, these effects varied greatly among individuals (Raap et al. 2015; 2016b). Experimentally exposing roosting individuals to ALAN presents them with an immediately challenging situation and the observed among-individual differences in ALAN-induced disruption in sleep behaviour might hence reflect differences in personality type. The most intuitive, but untested, hypotheses in this regard is that slow explorers, compared to fast explorers, will be more likely to avoid exposure to light at night when making roosting decisions and/or will be more disrupted in their sleep behaviour when challenged with light inside their nest box. Sleep is an important and widespread animal behaviour and, although its functions remain poorly understood, it seems to serve multiple crucial purposes including energy conservation and memory consolidation (reviewed in Siegel 2008; Rattenborg et al. 2017; Tougeron and Abram 2017). Given the importance of sleep and the fact that the disruptive effects of ALAN on sleep behaviour can be highly variable among individuals (Raap et al. 2015; 2016b), it is important to understand what causes this variation.

In this study, we tested the hypothesis that individual differences in exploration behaviour predict how individuals respond to a novel object and to ALAN in the context of roosting decisions and sleep behaviour. First, both as a metric of the response to a novel object, and as a means of assessing the potential for sampling bias in our subsequent analysis, we examined whether slow exploring great tits were less likely to roost in a nest box with a camera installed, as previously reported in another population (cf. Stuber et al. 2013). Second, we

120   examined whether slow explorers were less likely to roost in a nest box when confronted with

121   artificial light inside, representing a modified and novel roosting environment. Third, of those

122   individuals that did roost in a nest box with artificial light, we examined whether sleep

123   behaviour was more disrupted in slow explorers when challenged with ALAN than in fast

124   explorers.

Methodology

Study population and standard procedures

125 **Methodology**

126 *Study population and standard procedures*

127   We collected data in a resident semi-urban nest box population of great tits (about 150

128 nest boxes in total depending on the year and occurrence of vandalism) in the surroundings of

129 Wilrijk, Belgium (51°9'44''N, 4°24'15''E), which has been continuously monitored since 1997

130 (see e.g. Van Duyse et al. 2000; Casasole et al. 2017; Raap et al. 2017a; Thys et al. 2017). The

131 great tits used in this study were caught inside nest boxes during previous winter and breeding

132 seasons, and were sexed and ringed after capture. Since 2011 all adults have been provided with

133 a ring or implant containing a PIT tag (passive integrated transponder), thereby enabling the

134 detection of individual birds without physical disturbance when they are roosting inside nest

135 boxes. Age was determined using either hatching records or colour differences of primary

136 coverts to distinguish yearlings (grey) from older birds (bluish; Gosler 1993). Great tits are an

137 important model system for evolutionary and environmental research. Because they readily

138 sleep in nest boxes, we can study their sleep behaviour in the wild and experimentally

139 manipulate the light conditions to which they are exposed to during the night (Raap et al. 2015).

140

141 *Exploration behaviour in a novel environment*

142   We tested birds for their exploration behaviour as described in Dingemanse et al. (2002).

143 In brief, birds roosting in nest boxes in the winters (November - February) of 2010 until and

144 including 2015 were caught and transported to the laboratory. The morning after capture,

145 individuals were released separately into a novel environment room (4.0 x 2.4 x 2.3 m)

146 containing five artificial trees. We used the total number of flights and hops within two minutes

147 upon arrival in the room to calculate exploration scores (Dingemanse et al. 2002). Low and

148 high scores represent slow and fast explorers, respectively. Following the test, standard

149   morphometric measurements (wing length, tarsus, body mass) were taken and birds where

150   released near the nest box where they had been captured. Exploration behaviour is repeatable

151   in our population ($R = 0.40$; Thys et al. 2017), but since exploration scores have been shown to

152   increase with repeated testing (Dingemanse et al. 2012; Stuber et al. 2013; Thys et al. 2017),

153   we used only the first measured exploration score (i.e. exploration behaviour in a completely

154   novel environment) for those individuals that were tested multiple times.

155

156   *Novel object test*

157   Novel object (miniature video camera inside nest box) tests were performed during the

158   winters (November - February) of 2011 until and including 2015. On the first night, prior to the

159   installation of the video camera, the presence and identity of sleeping great tits was checked

160   with a handheld transponder reader (FR-250 RFID Reader, Trovan, Aalten, Netherlands). The

161   next day, miniature infrared sensitive video cameras (Pakatak PAK-MIR5, Essex, UK;

162   dimension 4 x 4 x 3.5 cm, colour: black) were installed under the nest box roof lid (similar to

163   Stuber et al. 2013). Cameras were installed at least two hours before sunset and removed at the

164   earliest about an hour after sunrise the next morning. We had data on both exploration behaviour

165   and the response to the novel object for 86 individuals. This specific dataset was used to

166   examine whether slow explorers were less likely to roost in a nest box when confronted with a

167   camera inside, similar to Stuber et al. (2013). We used only the first response to the novel object

168   for those individuals that were tested multiple times. The median number of days between novel

169   environment and novel object test was 97, the shortest period between tests was six days. On

170   three occasions the novel environment exploration test was performed after the novel object

171   test (12 days later at the earliest).

172

Exposure to ALAN and recording sleep behaviour

174   We constructed a second dataset in which we combined data on exploration behaviour

175   with data from our previous experimental studies on sleep behaviour and the response to ALAN

176   (Raap et al. 2015; 2016b; Sun et al. 2017). The experimental procedure was generally as

177   follows. Individuals served as their own control in all experiments. Video recording and

178   experimental light systems were installed at least two hours before sunset, when great tits

179   normally go to roost (Stuber et al. 2015b). During the first night when sleep behaviour was

180   recorded, birds slept in a dark nest box. During the second night of recording, a broad spectrum

181   white LED light (15 x 5 mm, taken from a RANEX 6000.217 LED headlight, Gilze,

182   Netherlands) secured underneath the nest box roof lid was turned on at least 2 hours before

183   sunset when great tits enter their nest box (see for details Raap et al. 2015; 2017b), producing

184   a modified and novel roosting environment. This approach ensures effective exposure to the

185   light treatment, which is crucial when exposing animals in the wild to ALAN (Raap et al.

186   2017c). Our earlier studies during the winter (Raap et al. 2015) and nestling season (Raap et al.

187   2016b) both used a light intensity of 1.6 lux, while data from Raap et al. (2017b) includes

188   observations obtained with a 3 lux light intensity. However, no differences in the response in

189   sleep behaviour were found between 1.6 and 3 lux (Raap et al. 2017b). Our experimental

190   approach with ALAN inside the nest box is not intended to mimic levels of ambient light

191   pollution that animals inside cavities/nest boxes could be exposed to. However, street lighting

192   can easily be more than 10 times as bright (10 - 40 lux; Gaston et al. 2017) as the intensity we

193   used in our experiments on sleep behaviour (1.6 and 3.0 lux; Raap et al. 2015; 2016b),

194   indicating that animals outside cavities/nest boxes can be exposed to similar intensities (see e.g.

195   Dominoni et al. 2013). In our population, nest boxes located near (≤16m) street lights

196   experience light intensities of 1.6 lux and up to ≈8 lux at the front of the nest box opening (Raap

197   et al. 2018b). Moreover, this field-based experimental approach with free-living animals

198   (contrary to laboratory studies) can offer useful insights into behavioural and physiological

199   effects of ALAN on wild animals (Raap et al. 2016a; 2016c; 2018a), especially since sleep

200   behaviour differs between captive and free-living animals, with great tits sleeping less in

201   captivity (Stuber et al. 2015b).

202   To examine whether exploration behaviour was associated with the likelihood to roost

203   in a nest box with ALAN inside (i.e. a modified roosting environment), we used winter data

204   from our 2015 and 2017 publications (Raap et al. 2015; 2017b; Sun et al. 2017), including all

205   individuals that slept in the nest box under natural dark conditions the first night and were

206   confronted with ALAN inside their nest box the following night ($N = 68$). Data from the

207   experiment performed during the breeding season (Raap et al. 2016b) was omitted from this

208   analysis, as the motivation to enter the nest box greatly differs when individuals need to take

209   care of their nestlings compared to the winter period.

210   To examine whether exploration behaviour was associated with the degree to which

211   ALAN disrupted sleep behaviour, we used all observations of sleep behaviour from individuals

212   that slept inside a nest box with a light inside ($N = 47$ of which there was exploration data

213   available for $N = 41$). This includes data on sleep behaviour from both the winter and nestling

214   season (Raap et al. 2015; 2016b; 2017b; Sun et al. 2017). We recorded sleep behaviour because

215   great tits are too small to be fitted with modern data loggers for recording brain activity

216   (necessary for conclusively defining sleep). Although using this proxy for sleep has its

217   limitations (Aulsebrook et al. 2016), it can be considered to be ecologically relevant as it has

218   been linked to amongst others, predation risk and extra pair paternity, and has a genetic basis

219   (Christe et al. 1996; Tripet et al. 2002; Steinmeyer et al. 2010; 2013; Stuber et al. 2014; 2015b;

220   2015a; 2016; 2017). Moreover, in blackbirds behaviourally observed and electrophysiological

221   measured sleep shows close correspondence (Szymczak et al. 1993). In great tits, sleep

222   disruption resulted in recovery sleep the following night (sleep rebound; Raap et al. 2016b)

223 indicating that sleep behaviour is associated with important functions which cannot be

224 performed otherwise (Lesku and Rattenborg 2014). Sleep phases and sleep intensity can be

225 studied in great detail by recording brain activity, while behavioural observation is less accurate

226 and more limited to measuring quantity. However, the latter is also less invasive and enables

227 the study of sleep in small free-living animals (Aulsebrook et al. 2016). Behaviourally observed

228 sleep in this study is limited to the time that the birds spent in the nest box. Although we cannot

229 quantify daytime sleep, this is likely to be minimal in this diurnal bird due to considerations

230 such as the demands of foraging for food in harsh winter conditions and the need to provide for

231 nestlings during the breeding season. Based on the findings in our previous studies we focussed

232 here on the sleep parameters awakening time and sleep duration, since disruptive effects of

233 ALAN were strongest for these parameters and both were affected during the winter and

234 nestling season (Raap et al. 2015; 2016b; 2017b; Sun et al. 2017). Sleep duration is the time

235 between when an animal falls asleep for the first time in the evening and wakes up in the

236 morning before leaving the nest box, the latter referring to awakening time. The disruptive

237 effect of ALAN on sleep is quantified as the difference in sleep behaviour during the first

238 control night and the second night when birds were challenged with ALAN. As in other sleep

239 behaviour studies on birds (Christe et al. 1996; Tripet et al. 2002; Steinmeyer et al. 2010; 2013;

240 Stuber et al. 2014; 2015b; 2015a; 2016; 2017), we defined an individual as asleep when the bird

241 was in the typical sleep position, with the beak pointing backwards and tucked under the

242 scapulars (Amlaner and Ball 1983).

243

244 *Statistical analysis*

245 All statistical analyses were performed in R 3.3.2 (R Core Team 2016) and were

246 performed in three steps:

247   1)   Is exploration behaviour associated with the likelihood to roost in a nest box with a

248   novel object (camera)?

249 First, we established that our dataset ($N = 86$) formed a representative sample of our study

250 population regarding exploration behaviour. That is, the frequency distribution of exploration

251 scores in the dataset used in the subsequent analysis was not different from that of the whole

252 population ($N = 621$, including only the first measured exploration score per individual; Fisher's

253 exact test $p = 0.29$; bin width = 5; Supplementary Fig. S1 & S2a; absolute numbers of

254 individuals per exploration score bin are provided in Table S1).

255   To determine whether the likelihood to roost in a nest box with a camera was related to

256 exploration score we constructed a generalized linear model (GLM) with binomial error

257 distribution and logit-link function (lme4 package; Bates et al. 2015). Whether or not birds

258 entered the nest box was the response variable and the model included sex as a factor and tarsus

259 length (size) and exploration score as standardized covariates (cf. Stuber et al. 2013).

260

261   2) Is exploration behaviour associated with the likelihood to roost in a nest box when

262   confronted with ALAN inside?

263 Our second dataset ($N = 68$) also formed a representative sample of our study population

264 regarding exploration behaviour (no differences in frequency distributions: Fisher's exact test

265 $p = 0.73$; Supplementary Fig. S1 & S2c; Table S1). Of the 68 individuals that slept in the nest

266 box under natural dark conditions the first night and were confronted with ALAN the second

267 night, there were only nine for which we had more than one observation of whether they entered

268 the nest box with ALAN inside. Hence, due to the small proportion of repeated measures

269 compared to the overall sample size, we could not use repeated measures in our statistical

270 analysis as model assumptions could not be met (Bolker et al. 2009). We therefore chose to use

271 only the first observation of whether a bird entered the nest box, reflecting the initial response.

272   To determine whether the likelihood to roost in a nest box when confronted with ALAN

273 inside was related to exploration score we constructed a generalized linear model (GLM) with

274 binomial error distribution and logit-link function. Whether or not birds entered the nest box

275 was the response variable and the model included sex as a factor and exploration score as a

276 standardized covariate.

277

278   3) Is exploration behaviour associated with the degree to which ALAN disrupts sleep

279   behaviour?

280 Our past experiments showed that ALAN in winter affected awakening time and sleep duration,

281 which were also affected during the nestling period (Raap et al. 2016b). Therefore, we focused

282 on those effects in this analysis, which also helps avoid multiple testing. Since the degree of

283 disruption by ALAN has been shown to differ between periods (winter versus nestling period;

284 Raap et al. 2016b), we standardized sleep parameters per period.

285   The relationship between the disruption in sleep behaviour by ALAN and exploration

286 score was then modelled using linear models with either awakening time or sleep duration as

287 the response variable. Both models included sex and age (first-year versus older) as a factor and

288 exploration score as a standardized covariate.

289   GLMs were checked for overdispersion by comparing the residual deviance to its

290 degrees of freedom. The normality of residuals assumption was assessed for linear models. The

291 sim function (package arm, Gelman et al. 2015) was used throughout to simulate values (2000

292 simulations) of the posterior distribution of all model parameters. Results are presented as

293 estimated means with 95% credible intervals (CrI), unless stated otherwise, and effects were

294 considered significant in the frequentist sense when CrIs did not overlap zero.

295

296 *Ethics*

297   We compiled a dataset from previous experiments and behavioural data and therefore

298 did not need to expose new individuals to experimental treatments. All experiments were

299 approved by the ethical committee of the University of Antwerp (ID number 2014-45),

300 performed in accordance with Belgian and Flemish laws, and adhered to the ASAB/ABS

301 guidelines for the use of animals in behavioural research and teaching. The Belgian Royal

302 Institute for Natural Sciences provided ringing licenses for all authors and technicians. Because

303 of the short duration of the manipulation (one night of artificial light per experiment) the

304 disturbance was assumed to be minimal.

305 Data accessible at Zenodo doi: 10.5281/zenodo.1254850

Results

1) Is exploration behaviour associated with the likelihood to roost in a nest box with a novel object (camera)?

Exploration score was not associated with the likelihood to roost in a nest box with a camera (Table 1; Supplementary Fig. S3). The relative frequency distribution of exploration scores in the population (individuals roosting in nest boxes) was similar before and after camera installation (Fisher's exact test $p = 1$; Supplementary Fig. S2a & b; Table S1). Nonetheless, the percentage of individuals that roosted in the nest box when a camera was present dropped to 81%. Overall, there were no size (tarsus length) or sex differences in the likelihood to enter the nest box with a camera (Table 1), with a mean likelihood of 0.89 for females and 0.73 for males.

2) Is exploration behaviour associated with the likelihood to roost in a nest box when confronted with ALAN inside?

Exploration score was not associated with the likelihood to roost in a nest box with ALAN inside (Table 2; Supplementary Fig. S4). The relative frequency distribution of exploration scores in the population (individuals roosting in nest boxes) was similar before and after turning on the light inside the nest box (Fisher's exact test $p = 0.99$; Supplementary Fig. S2c & d; Table S1). Nonetheless, the percentage of individuals that roosted in the nest box with ALAN inside dropped to 71% (67% entered in winter 2014, $N = 27$; 73% entered in winter 2015, $N = 41$). Overall, there were no sex differences in the likelihood to enter the nest box with ALAN inside (Table 2), with a mean likelihood of 0.67 for females and 0.74 for males.

328   *3) Is exploration behaviour associated with the degree of disruption in sleep behaviour*

329   *when challenged with ALAN?*

330 Exploration score was not associated with the degree of disruption in sleep behaviour when

331 challenged with ALAN. That is, neither the response in awakening time, nor the response in

332 sleep duration was predicted by exploration score (Table 3; Fig. 1). Overall, there were no

333 differences between the sexes or age classes (first-year versus older) in the degree of sleep

334 disruption by ALAN (Table 3).

Discussion

We show that the disruptive effects of artificial light at night on sleep behaviour (awakening time and sleep duration) were not associated with individual differences in exploration behaviour, as a proxy of personality variation, in free-living great tits. Contrary to expectations and findings in Stuber et al. (2013), we found that slow and fast explorers were equally likely to roost in a nest box with a camera inside, as well as equally likely to enter a nest box when confronted with ALAN inside. Hence, although the overall percentage of birds roosting in their nest box decreases after installation of a camera or light, we found no evidence for personality-dependent sensitivity to the novel object or avoidance of artificial light when making roosting decisions. Consequently, no sampling bias arose due to this experimental treatment. In the following paragraphs, we discuss our results and their possible implications.

No evidence for personality-dependent sampling bias or avoidance of ALAN

We found no evidence that confronting great tits with a camera or LED light inside their nest box resulted in a personality-dependent sampling bias or avoidance of artificial light, since slow and fast explorers were equally likely to roost in their nest box in both cases. This contradicts predictions since, compared to fast explorers, slow exploring great tits are generally found to be less willing to approach and accept novel objects (e.g. Verbeek et al. 1994; Carere et al. 2005; Stuber et al. 2013; Cole and Quinn 2014; Baugh et al. 2017), and are expected to be more sensitive to anthropogenic disturbances and modifications of the environment (Sih et al. 2012; Lowry et al. 2013; Naguib et al. 2013).

Indeed, Stuber et al. (2013) previously found that slow exploring great tits were less likely than fast explorers to roost inside a nest box when confronted with a novel object (camera), demonstrating exploration behaviour-related sampling bias. Along this line, there is

growing empirical evidence for animal personality resulting in sampling bias (e.g. Garamszegi et al. 2009; Carter et al. 2012; Niemelä et al. 2015), indicating that this problem is widespread and can have important implications for conclusions drawn from ecological studies (Biro and Dingemanse 2009). Here, however, we did not find such evidence. First of all, it is important to note that differences in findings with Stuber et al. (2013) are unlikely to be due to sample size related power issues. Specifically, the small effect size ($\beta = -0.18$; compared to $\beta = 0.88$ in Stuber et al. 2013) of exploration score on the likelihood to roost inside a nest box when confronted with a novel object or ALAN, in combination with credible intervals that are far from overlapping zero (see Tables 1 & 2), strongly suggest the absence of exploration behaviour-dependent responses to novelty and ALAN in our population.

There are several possible ecological and evolutionary explanations for the discrepancy in results with Stuber et al. (2013), such as differences among populations. Of particular note, Stuber et al. (2013) studied a rural population of great tits, whereas our study was done in a semi-urban population. Increasing evidence suggests that the level of urbanization can influence behaviour, both within and among species (Wong and Candolin 2015), and that more exploratory, bolder behavioural phenotypes might be more successful in settling in more urbanized environments (review in Lowry et al. 2013). Hence, the difference in findings with Stuber et al. (2013) could be caused by the overrepresentation of fast exploring, bold individuals in our semi-urban population. However, this was not the case, as the relative frequency distributions of exploration behaviour in both populations seem very similar, and if anything, slow explorers might be more represented in our population (relative frequency exploration score 0-5: our population ≈ 0.42, Supplementary Fig. S2; Stuber et al. 2013 ≈ 0.23).

Another possibility is that differences in selection pressures between (semi-) urban and rural environments influence the relationship between exploration behaviour and the response to novelty (Sih et al. 2012). Higher human disturbance levels in our population (relative to rural

populations) might result in habituation to disturbance and/or select for on average less neophobic birds (Tryjanowski et al. 2016), regardless of differences in exploration behaviour. This explanation is also in line with our finding that different personality types did not differ in their willingness to roost inside a nest box when confronted with light inside, representing a modified and novel roosting environment. Along this line, a recent study in great tits demonstrated that individual differences in exploration behaviour were not associated with variation in urbanization features of the breeding territory, including artificial light (Charmantier et al. 2017). Together this suggests that, in great tits, artificial light does not appear to influence behavioural phenotypes differently when making decisions about breeding and roosting locations. However, whether ambient light conditions (e.g. artificial light due to street lights), instead of experimental exposure, influences personality-dependent roosting decisions in free-living birds remains to be determined. In addition, whether particular behavioural trait associations are indeed influenced by urbanization (e.g. Scales et al. 2011; Bokony et al. 2012), and whether this is due to phenotypic plasticity (e.g. habituation) and/or adaptive evolution, requires further research (see e.g. Miranda et al. 2013; Charmantier et al. 2017).

Finally, it should be noted that occupancy of a nest/roost site depends on many factors such as availability of natural cavities and nest boxes and that great tits (and other cavity nesting species) are not entirely "free" to choose where to roost. The availability of natural cavities might be relatively low in our population (compared to rural populations), leaving less alternatives for roosting sites and increasing motivation to use nest boxes, despite potentially suboptimal conditions (due to our experimental treatments). This might also explain why the percentage of birds entering the nest box with a novel object inside is higher in our population (81%) compared to the population of Stuber et al. (2013; 60%).

No evidence for personality-dependent effects of ALAN on sleep behaviour

We find no evidence that ALAN induces personality-dependent effects on sleep behaviour, since sleep behaviour of slow and fast explorers was equally disrupted. This contradicts predictions since more exploratory and bolder individuals are generally expected to be better able to cope with challenges and to have a higher tolerance to disturbance (e.g. Lowry et al. 2013), and hence could be less disrupted in their sleep behaviour when challenged with ALAN. Specifically, fast exploring great tits are predicted to be more successful in inhabiting disturbed environments, including those with high levels of (light) pollution. In line with this prediction, when compared to fast explorers, slow exploring great tits were more disturbed by noise, taking longer to restart feeding their nestlings after the initiation of experimental playback (Naguib et al. 2013). Moreover, rural great tits have been found to be less exploratory and more neophobic than their urban counterparts (Tryjanowski et al. 2016; Charmantier et al. 2017) suggesting that slow exploring and neophobic individuals are less successful in inhabiting environments with higher anthropogenic disturbance. Similarly, in another study on great tits, bold individuals (with boldness measured as flight initiation distance) were overrepresented in areas with more cars and fewer pedestrians, while shy individuals were more likely to be found in areas with less cars and more pedestrians (Sprau and Dingemanse 2017). However, another recent study showed that great tits in metal polluted areas were, on average, less exploratory than their conspecifics in areas with less metal pollution (Grunst et al. 2018). This, together with our finding that slow and fast exploring great tits are equally disrupted in their sleep behaviour when challenged with ALAN, highlights that the sensitivity to disturbance of different behavioural types might depend on the behavioural context and the specific type of disturbance or component of urbanization in question, making broad generalizations difficult.

To the best of our knowledge, this is only the first study to assess whether the degree of behavioural disruption by ALAN is dependent on the personality type of free-living animals

434   and therefore there are many opportunities for further research. First, our light treatment

435   consisted of a single night, while light pollution is a long-term disturbance. Hence, we cannot

436   exclude the possibility that long-term exposure to ALAN might result in personality-dependent

437   avoidance or other behavioural and physiological responses. Indeed, laboratory and aviary

438   experiments suggest that habituation towards ALAN is unlikely, as has for example been

439   demonstrated in peahens (*Pavo cristatus*; Yorzinski et al. 2015). Moreover, light exposed great

440   tits in a laboratory experiment actually showed increased effects on nightly activity during

441   longer-term exposure to ALAN (de Jong et al. 2016). Due to differences in behaviour and

442   especially sleep behaviour between captive and wild animals (Stuber et al. 2015b; Aulsebrook

443   et al. 2016) it will be of interest to examine effects of long-term exposure to ALAN in free-

444   living great tits. Second, our light treatment does not attempt to mimic natural variation in the

445   light conditions experienced by cavity nesting species at night (see also Methodology). Hence,

446   while we find that differences in exploration behaviour do not affect an individuals' roosting

447   decision when confronted with ALAN inside a nest box, the extent to which ambient light

448   conditions affects personality-dependent roosting decisions in the wild remains to be

449   determined. Another interesting question is whether avoidance behaviour when confronted with

450   ALAN depends on personality type in other populations, given increasing evidence that

451   population differences might occur (Tryjanowski et al. 2016), as for example found here for the

452   response to a novel object between our semi-urban population and the rural population used by

453   Stuber et al. (2013). Third, although we found no evidence that the degree of disruption by

454   ALAN in sleep behaviour is dependent on exploratory personality type, future studies should

455   extend this work to include other relevant personality traits and other behaviours known to be

456   affected by ALAN. Finally, while our study is based on a widely used model species,

457   differences in response to ALAN may occur even between closely related species (Sih et al.

458   2012). For example, earlier we found that ALAN differentially affects the sleep behaviour of

congeneric blue and great tits, with blue tits hardly being affected by ALAN, in contrast to great tits (Sun et al. 2017). Hence, whether differences in personality-dependent responses to ALAN occur between even closely related species requires further research. If ALAN does differentially affect certain behavioural or physiological phenotypes across ecologically relevant contexts, this might have cascading effects on energy balance and fitness, and might affect population dynamics in urbanized and light polluted areas (Sih et al. 2012; Wong and Candolin 2015).

Conclusions

Slow and fast personality types were equally disrupted in their sleep behaviour when challenged with ALAN. Furthermore, experimentally confronting birds with a light inside the nest box to study the effects of ALAN did not cause personality-dependent sampling bias or avoidance behaviour. Therefore, this setup ideally bridges the gap between laboratory and field studies exploring fundamental questions about the effects of ALAN in free-living birds. However, our results need to be validated as personality-dependent effects of ALAN and other anthropogenic stressors could differ between populations and species. Moreover, although there is increasing evidence that behavioural phenotypes can differ in their response to anthropogenic modifications of the environment, our findings highlight that effects might be specific to the behavioural context and type of disturbance. In our increasingly urbanized world, determining whether the effects of anthropogenic disturbances and modifications depend on behavioural type will hence be of paramount importance, given it may affect population dynamics in urbanized and light polluted areas.

481 **Competing interests**

482 We have no competing interests.

483

484 **Author Contributions**

485 TR, BT, RP and ME conceived and designed the study. TR, BT, ASG, MLG carried out the

486 fieldwork; TR and BT wrote the first draft. All authors contributed critically to the drafts and

487 gave final approval for publication.

488

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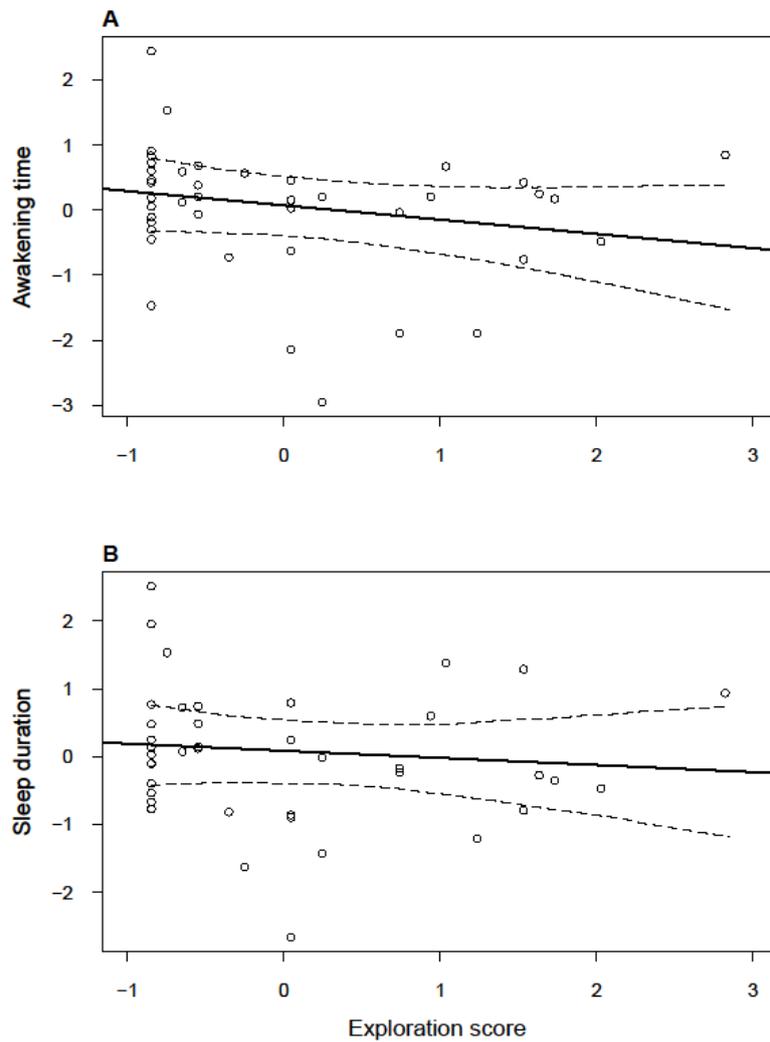
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Figure caption

Figure   1

Disruptive effects of artificial light at night on sleep behaviour were not personality-

dependent. Slow and fast explorers were equally disrupted by ALAN in awakening time (A)

and sleep duration (B). Exploration score (standardized) in relation to the disruption by ALAN,

average regression line (bold) including the 95% credible interval (dashed lines). Observations

are shown in circles ($N = 41$).

Tables

723 *Table 1:* Predictors of the likelihood to enter the nest box with a camera ($N = 86$). Point estimates (β)
724 are given with 95% credible intervals (CrI).

	β^a	q2.5%[b]	q97.5%[b]
Intercept	2.16	1.17	3.19
Sex[c]	-1.16	-2.50	0.23
Tarsus	0.54	-0.12	1.22
Exploration score	-0.18	-0.75	0.41

[a] estimated mean of the posterior distribution
[b] 2.5% and 97.5% quantiles of the posterior distribution (95% CrI)
[c] female as reference category

725

726 ***Table 2:*** Predictors of the likelihood to enter the nest box with ALAN inside ($N = 68$). Point estimates
727 (β) are given with 95% credible intervals (CrI).

	β[a]	q2.5%[b]	q97.5%[b]
Intercept	0.73	-0.04	1.49
Sex[c]	0.30	-0.82	1.35
Exploration score	-0.18	-0.71	0.34

[a] estimated mean of the posterior distribution
[b] 2.5% and 97.5% quantiles of the posterior distribution (95% CrI)
[c] female as reference category

728

729 ***Table 3:*** Predictors of the degree of disruption by ALAN on Awakening time and Sleep duration ($N =$
730 41). Point estimates (β) are given with 95% credible intervals (CrI).

	Awakening time			Sleep duration		
	β[a]	q2.5%[b]	q97.5%[b]	β[a]	q2.5%[b]	q97.5%[b]
Intercept	0.07	-0.31	0.53	0.09	-0.33	0.55
Sex[c]	0.09	-0.61	0.80	0.07	-0.64	0.74
Age[d]	-0.22	-0.88	0.47	-0.25	-0.91	0.44
Exploration score	-0.21	-0.53	0.13	-0.10	-0.45	0.23

[a] estimated mean of the posterior distribution

[b] 2.5% and 97.5% quantiles of the posterior distribution (95% CrI)

[c] female as reference category

[d] first-year as reference category

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