

1 Manuscript: Light pollution at the urban forest edge and its impact on insectivorous bats

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5 Abstract

6 Connectivity and quality of vegetation in cities, including urban forests, can promote urban
7 biodiversity. However the impact of anthropogenic pressures at the forest-matrix edge, particularly
8 artificial light at night (ALAN), on connectivity has received little attention. We assessed the
9 influence of artificial light at forest edges on insectivorous bats. We acoustically surveyed 31 forest
10 edges across greater Sydney, Australia, half with mercury vapour streetlights and half in ambient
11 darkness, and compared the bat assemblage and activity levels to urban forest interiors. We also
12 sampled the flying insect community to establish whether changes in insect densities under lights
13 drive changes in insectivorous bat activity. We recorded 9965 bat passes from 16 species or species
14 groups throughout our acoustic survey. The activity of all bats, and bats hypothesised to be
15 sensitive to artificial light, was consistently higher in forest interiors as opposed to edges. We found
16 that slower flying bats adapted to cluttered vegetation or with a relatively high characteristic
17 echolocation call frequency; *Chalinolobus morio*, *Miniopterus australis*, *Vespadelus vulturnus*, and
18 *Nyctophilus* spp., were negatively affected by artificial light sources at the forest edge. The
19 emergence time of *Vespadelus vulturnus* was also significantly delayed by the presence of
20 streetlights at the forest edge. Conversely, generalist faster flying bats; *Chalinolobus gouldii*,
21 *Ozimops ridei*, *Austronomus australis*, *Saccolaimus flaviventris*, and *Miniopterus orianae oceanensis*,
22 were unaffected by artificial light at the edge of urban forest, and used light and dark forest edges
23 in a similar way. Insect surveys showed that larger lepidopterans seemed to be attracted to lit areas,
24 but in low numbers. Artificial light sources on the edges of urban forest have diverse effects on bats

25 and insects, and should be considered an anthropogenic edge effect that can reduce available
26 habitat and decrease connectivity for light-sensitive species.

27 1. Introduction

28 Urbanisation is one of the leading causes of biodiversity loss worldwide (Czech et al. 2000,
29 McKinney 2006). Habitat fragmentation (Fischer and Lindenmayer 2007), along with noise pollution
30 (Ortega 2012), air pollution (Leonard and Hochuli 2017), reduced water quality (Blakey et al. 2018),
31 reduced vegetation cover and structure (Threlfall et al. 2016, Threlfall et al. 2017) and artificial light
32 (Hölker et al. 2010) all contribute to degrading natural habitat for urban wildlife. Although only
33 taking up a small percentage of the planet's terrestrial surface, urbanised areas are predicted to
34 grow by 1.2 million km² by 2030, impacting many global biodiversity hotspots (Seto et al. 2012).
35 Hence, investment in the conservation of urban biodiversity is essential for many reasons (Dearborn
36 and Kark 2010).

37 Providing "stepping stones and corridors" of forests and native vegetation is a commonly suggested
38 conservation action for urban biodiversity (Dearborn and Kark 2010, Beninde et al. 2015).

39 Connecting forest habitat in cities can mitigate species loss and biotic homogenisation
40 (Lindenmayer and Nix 1993, Fischer and Lindenmayer 2007) by facilitating movement (Dearborn
41 and Kark 2010) and genetic diversity (Aguilar et al. 2008) of native animals across a degraded urban
42 landscape. Over the last few decades, research has focused on quantifying the characteristics of
43 habitat remnants that maximize their value to native plants and animals, including their size (Evans
44 et al. 2009), shape (Hawrot and Niemi 1996), and connectedness (Keitt et al. 1997, McGarigal et al.
45 2002, Beninde et al. 2015). Calculating the amount of viable habitat existing in urban areas is a more
46 complex process. It must incorporate not only structural elements of forest areas, such as their size
47 and shape, but also functional connectivity (Kupfer 2012), and whether structural habitat features
48 are actually used. Anthropogenic pressures, such as ALAN, may impact functional connectivity

49 (Hale et al. 2012) by narrowing wildlife corridors and reducing functional patch sizes, however, the
50 extent to which this occurs is poorly understood currently.

51 ALAN is a growing problem, escalating by 6 % each year (Hölker et al. 2010). It is caused by
52 illumination from anthropogenic lighting, and is most prevalent in urban areas (Falchi et al. 2016).
53 Only relatively recently has ALAN been widely discussed as a global threat to biodiversity (Rich and
54 Longcore 2013, Gaston et al. 2015). Streetlights disrupt migration patterns (La Sorte et al. 2017),
55 breeding cycles (Navara and Nelson 2007) and predator-prey interactions (Gorenzel and Salmon
56 1995). Streetlights may also have an effect on the functional value and connectivity of proximal
57 urban forests and vegetation. Streetlights positioned along edges of urban wildlife corridors
58 negatively affect some species whilst attracting others (Azam et al. 2018). The effects of artificial
59 light at the forest edge for nocturnal wildlife may be significant; light may penetrate dark
60 vegetation anywhere from 50 m (Kempenaers et al 2010) to 380 m (Pocock and Lawrence 2005).
61 Dark habitats are currently at risk from the edge effects of ALAN.

62 Insectivorous bats are an ecologically diverse group, and respond in a variety of ways to
63 urbanisation (Russo and Ancillotto 2015). Some faster flying open-space adapted bat species find
64 roosts in buildings (Kunz 1982) and can commute across urbanised landscapes (Jung and Kalko
65 2011). Conversely, other slower flying clutter-adapted bat species commonly avoid urban areas,
66 they cannot adapt to changes in roost availability and instead are reliant on networks of urban
67 forest to survive in cities (Basham et al. 2011). Artificial light is one anthropogenic pressure driving
68 these diverse responses to urban areas. Ultraviolet radiation attracts high numbers of insects (van
69 Grunsven et al. 2014) and could offer urban feeding grounds for faster flying bat species adapted to
70 exploit this resource (Rydell 1992, Rydell and Racey 1995). These bats may be able to dive through
71 the light cone when foraging (Blake et al. 1994) and perhaps able to evade any aerial predators that
72 use the lit areas as hunting grounds. Conversely, slower flying clutter-adapted species often avoid
73 artificially lit areas (Stone et al. 2012) and may be constrained by lights at the patch edge, spending

74 a majority of their foraging time within dark patches (Threlfall et al. 2013, Hale et al. 2015), and
75 therefore reducing their functional urban habitat. Artificial light also markedly delays some species'
76 emergence times from roosts (Jones and Rydell 1994, Downs et al. 2003, Boldogh et al. 2007),
77 meaning that their foraging time is reduced and the health of the population may at risk (Boldogh
78 et al. 2007). There is a global pattern emerging that ALAN negatively affects species adapted to
79 foraging in either cluttered vegetation or along habitat edges, like *Rhinolophus hipposideros* (Stone
80 et al. 2012), *Eptesicus serotinus* (Azam et al. 2018), and *Nyctophilus gouldi* (Threlfall et al. 2013). The
81 mechanistic drivers of this light phobia in bats are not completely understood (Stone et al. 2015,
82 Rowse et al. 2016) but could include predator avoidance (Speakman 1991, Stone et al. 2009, Lima
83 and O'Keefe 2013), morphology that leaves slower flying bats less able to exploit airborne insect
84 prey at lights compared with faster flying bats like *Pipistrellus pipistrellus* (Haffner and Stutz 1985)
85 sensitivity to ultraviolet radiation emitted by some streetlights (Gorresen et al. 2015), or a
86 combination of these. Bats with many of these traits are declining in cities (Jung and Threlfall 2016,
87 Jung and Threlfall 2018) hence research on the impact of public lighting on this group is urgently
88 required.

89 We hypothesised that permanent streetlights along the forest edge would reduce the activity of
90 some insectivorous bats due to a decline in habitat quality. We predicted that the activity of bats
91 with slow flight speed would be lower at forest edges with streetlights than edges with no lights.
92 We also predicted that the activity of faster flying, light-exploiting bats would either be unaffected
93 or be higher at edges with streetlights than edges with no lights. Finally, we predicted that total bat
94 activity, and the activity of bats with slow flight speed, would both be higher in the forest interiors
95 than the forest edges.

96 2. Method

97 2.1 Site selection

98 Our survey was carried out in Greater Sydney, a sub-tropical city with a population of over 4.5
99 million, on the east coast of New South Wales, Australia. Sydney has much remnant native forest
100 abutting the urban matrix, both in continuous national parks and in smaller isolated patches
101 surrounded by housing (Benson et al. 1995). Two main geologies in the Sydney region, shale and
102 sandstone, have led to different levels of primary productivity and soil fertility across the city, and
103 these have been shown to influence insect prey and bat diversity in this region (Threlfall et al. 2011,
104 Threlfall et al. 2012). Hence, we only included sites on full or majority sandstone with transitional
105 soil type to control for this effect of geology.

106 *2.2 Experimental design*

107 We conducted an acoustic survey along 31 forest edge sites (Figure 1); 16 of these sites were at the
108 edges of connected forest (forest connected to large natural areas, Figure 2a), and 15 were on the
109 edges of isolated forest patches (Figure 2b), >30 ha in size, but surrounded on all sides by urban
110 matrix. Of all connected patch edge sites, half the sites (n=7) had 80W mercury vapour streetlights
111 along the edges (light intensity of $10.65 \text{ lux} \pm 1.89$) and half of the sites (n=8) were dark (light
112 intensity of $0.52 \text{ lux} \pm 0.34$). Of all forest patch edge sites, half the sites (n=8) had 80W mercury
113 vapour streetlights along the edges (light intensity of $10.20 \text{ lux} \pm 1.23$) and half of the sites (n=8)
114 were dark (light intensity of $0.97 \text{ lux} \pm 0.52$). All edge sites were defined as roads or pathways over
115 4m in width with dense vegetation on only one side. Dark edges were defined as 30m of
116 uninterrupted dark conditions (artificial light levels comparable to ambient darkness and no
117 external light sources on nearby houses). Artificially lit edges were defined as 30m of 80W mercury
118 vapour lights along one side of the road, with the streetlights at a median distance apart of 12.1m.
119 Usual low-level urban lighting from houses in the surrounding matrix was present at both dark and
120 light edges. We additionally located control sites in the dark interior of all 31 sites (lux of $0.55 \pm$
121 0.20), which were located along an internal edge comprising a pathway or track (2 m typical width)
122 between 400 m and 1 km perpendicular from the sampled forest edge. This allowed us to sample

123 the bat assemblage at 31 edge sites, and 31 dark interior control sites, leading to 62 sites in total.
124 We sampled between November and December of 2016, the maternity season for bats when
125 resource requirements and activity levels are highest. The light intensity (lux) at each site was
126 measured using a lux meter (QM1587; Reduction Revolutions Pty Ltd, Parramatta, Australia). We
127 also measured insect biomass at all forest patches, at both the interior and edge site, using a black
128 light intercept traps (Australian Entomological Supplies, Murwillumbah, Australia, see Appendix)

129 *2.3 Bat recording*

130 The acoustic survey was carried out using Anabat II detectors (Titley Electronics, Ballina, Australia)
131 placed on the ground with the high frequency microphone positioned 1 m above the ground and
132 pointing upwards at a 45° angle to record all echolocation calls of passing bats. We used one
133 detector per site, and predicted to still record high flying bats to be recorded due to louder calls
134 from those species (Jung and Kalko 2011). At artificially lit edges the detector was placed no further
135 than 3 m from the base of the streetlight pole, no more than 3 m away from the edge of the forest.
136 At both the edge and interior sites, the microphone was pointed parallel down the forest edge and
137 down the interior track or path, respectively, to optimise the amount of habitat sampled (Law et al.
138 1998, Threlfall et al. 2012). Each of the 62 sites were sampled between 3 – 5 consecutive nights
139 (average 4.35 nights \pm s.e. 0.19, due to unexpected equipment failure we did not manage to record
140 for 5 nights at each site), totaling 270 recording nights across the entire survey. A maximum of eight
141 sites were surveyed on the same night, where the edge and its respective interior control were
142 concurrently sampled. The detectors passed the data through a Zero-Crossings Interface Module
143 (ZCAIM; Titley Electronics). The acoustic files collected during the survey were processed using
144 Anascheme and a bat call identification key developed for Sydney bats (Adams et al. 2010). For a
145 bat call to be identified to species level, three or more pulses were required and have characteristics
146 that fall within the program's parameters for that species. A pass was defined as at least three valid
147 pulses with a minimum of 6 pixels per pulse. Successful species identifications were made only

148 when a minimum of 50% of pulses within a pass were identified as the same species (Adams et al.
149 2009, Threlfall et al. 2012). The calls identified as *Chalinolobus dwyeri*, *Falsistrellus tasmaniensis*,
150 *Nyctophilus* spp., *Saccolaimus flaviventris*, *Scoteanax rueppellii* and *Scotorepens orion* are known to
151 be complex or rare and were manually checked against known parameters and confirmed or re-
152 identified (Adams et al. 2010). In addition, calls were run through a species filter in AnaScheme
153 which is specifically designed to identify calls of *Chalinolobus gouldii* with alternating frequency. The
154 call characteristics of *Nyctophilus gouldi* and *Nyctophilus geoffroyi* are indistinguishable using the
155 AnaScheme method and so were pooled as one taxon; *Nyctophilus* spp. Only species that were
156 positively identified using the key, filters and manual checking were included for further analysis to
157 eliminate any bias caused by using partially identified species.

158 2.4 Assignment to functional groups

159 Assignment of each species to a functional group was based on morphological traits and foraging
160 styles (Rhodes 2002, Haddock et al. in press). *Chalinolobus gouldii*, *Ozimops ridei*, *Austronomus*
161 *australis*, *Saccolaimus flaviventris*, and *Miniopterus orianae oceanensis* were categorised as light-
162 exploiting due to their open-space foraging area preference, or edge-space foraging area
163 preference with low or medium echolocation call frequency (Rhodes 2002). Light-exploiting bats
164 may tend to use the well-lit areas to forage around or commute past. The light-sensitive group
165 consisted of both maneuverable edge-space foraging species with high echolocation call frequency
166 (*Chalinolobus morio*, *Miniopterus australis*, *Vespadelus vulturnus*; Adams et al. 2009) and also species
167 adapted to cluttered vegetation with a slower flight pattern (*Rhinolophus megaphyllus* and
168 *Nyctophilus* spp., consisting of two species *Nyctophilus gouldi* and *Nyctophilus geoffroyi* that have
169 echolocation calls indistinguishable from the other) that may avoid lit areas. We based these
170 groupings on known response groups found in previous studies, however we acknowledge that
171 there may be species that do not necessarily fit this trend.

172 2.5 Measurement of environmental variables

173 The percentage of native vegetation cover (>3 m tall) within a radius of 250m of each site was
174 calculated using Arc Map (ESRI, Redlands, USA, ver. 10.2) and was calculated through intersecting
175 GPS points of our sites with the GIS layer 'The Native Vegetation of the Sydney Metropolitan Area -
176 Version 3, VIS_ID 4489' (NSW Office of Environment and Heritage, Sydney). This area has been
177 found to be indicative of local habitat as shown in previous studies (Lacoeuilhe et al. 2014). The
178 same method was used to calculate the percentage of sandstone and transitional sandstone soil
179 type within the 250m radius of each site. Average moon illumination was calculated by noting the
180 percentage of the moon's face visible each night, and then for each site taking an average of the
181 percentages across all the nights sampled. Although we avoided surveying on full moon, logistical
182 limitations meant that we could not control for the moon cycle completely.

183 *2.6 Statistical analysis*

184 All analyses were carried out in SPSS (version 22, SPSS Inc., Chicago, USA). For each of the 31 sites
185 and their dark interior urban forest controls, average activity and total species richness was
186 calculated for the bat assemblage, for the light-exploiting functional group, for the light-sensitive
187 functional group and for each individual species. Average activity was calculated by summing the
188 total number of identified passes detected at that site during the recording time, and then dividing
189 by the number of sampling nights at that site. Total species richness was calculated by counting the
190 number of species detected at that site over the recording time. To calculate the time until first
191 activity, and therefore potential delay or disturbance to the bats, we located the earliest call for a
192 functional group or species at a particular site and then subtracted that time from the time of
193 sunset that day (EST), leaving the numbers of minutes after sunset that the call was recorded.
194 When discussing the comparison of a response variable across light treatments, we are including
195 light edges, dark edges and dark interiors.

196 Generalized linear models (GLMs) were used to establish statistical differences in both lux level and
197 vegetation extent between the three light treatments, with the habitat treatment (connected or
198 patch) and light treatment (light edge or dark edge) as fixed effects.

199 A series of correlations were used to assess whether average moon illumination across recording
200 time, or the percentage of sandstone soil within a 250 m radius of each site were significant
201 predictors of bat activity or species richness. As none were significant predictors of species richness
202 or total bat activity, they were omitted from further models. A series of GLMs were used to assess if
203 emergence times of *C. gouldii*, *O. ridei*, *V.vulturinus* and *Nyctophilus* spp. (the two most commonly
204 detected of each response group) were affected by moon illumination, moon illumination has been
205 linked to emergence of bats. As no response variables were significantly affected by any
206 environmental or weather variables, all were omitted from further models.

207 We then used a series of GLMMs to compare bat and insect response variables (Table 1) across light
208 treatments. We only included sites where both the edge and interior had a record for that species.
209 Other sites were excluded from this analysis. The GLMMs allowed us to include the site (which
210 contained both the edge and dark interior pair) as a random effect, and the habitat treatment
211 (connected or patch) and light treatment (light edge or dark edge) as fixed effects. We considered a
212 variety of response variables (Table 1). We then also carried out analyses on the two most
213 commonly recorded light-exploiting species; *C. gouldii* and *O. ridei*, and the two most commonly
214 recorded light-sensitive species; *V. vulturinus* and *Nyctophilus* spp. as activity of other species was
215 too low or too patchy in distribution to allow for adequate analysis.

216 We used Poisson distribution models with a log link function and robust variance estimates for all
217 but two of the GLMMs as the data did not follow a normal distribution (Yau and Kuk 2002), the
218 exceptions were light-sensitive bat activity and *Nyctophilus* spp. activity. Light-sensitive bat activity
219 was low across all treatments and so a negative binomial distribution with a log link function with
220 robust variance estimates was used in the GLMM. Soft-calling *Nyctophilus* spp. were recorded in

221 such low numbers that activity of this taxa was converted to presence-absence data, and a GLMM
222 was run using a binomial distribution with a probit link function, again with robust variance
223 estimates. All post hoc tests were Fisher's Least Significant Difference.

224 When light-sensitive or light-exploiting bats were detected at a site, we wanted to know what
225 proportion of the calls were detected along the edge compared to the interior for that site, as an
226 indicator of whether edges or interior were more preferred by each bat group. For each edge and
227 interior site pair, we therefore calculated the proportion of calls recorded at the forest edge
228 compared that site's interior control for both light-sensitive and light-exploiting functional groups.
229 A one way ANOVA was used to compare the proportion of calls recorded at light edges and at dark
230 edges for both light-exploiting and light-sensitive groups.

231 3. Results

232 We recorded 9965 bat passes throughout our acoustic survey, with 62.4% identified to species or
233 species group level. We detected 16 species or species groups, seven of which have a conservation
234 status of vulnerable under the NSW Biodiversity Conservation Act 2016; *Chalinolobus dwyeri*,
235 *Falsistrellus tasmaniensis*, *Miniopterus orianae oceanensis*, *Miniopterus australis*, *Micronomous*
236 *norfolkensis*, *Scoteanax rueppellii*, *Saccolaimus flaviventris*.

237 Artificially lit edges, dark edges and interiors all differed significantly from each other in the amount
238 of vegetation cover within 250 m of each site. Interior control sites had greater vegetation extent
239 than dark edges ($p < 0.005$), and light edges had greater vegetation extent than dark edges ($p <$
240 0.05). Forest patches had significantly less vegetation cover within a 250 m radius of each site than
241 connected forest ($p < 0.001$). Artificially lit edges were significantly brighter ($F_{2,59} = 157.9, p < 0.005$)
242 than dark edges ($p < 0.005$) and dark interiors ($p < 0.005$).

243 Echolocation calls of bats were recorded at all sites. Light-exploiting bat species were detected at
244 95% of sites; with 96% of edge sites and 93% of interior sites. Light-sensitive bat species were
245 detected at 51% of sites, including 41% of edge sites, and 61% at interior sites.

246 Total bat activity was significantly different among light treatments, with light edges and dark
247 edges having significantly lower activity than dark interior sites (Table 2). Total bat activity was not
248 significantly different between light and dark edges ($p > 0.05$; Figure 3a). Species richness was not
249 significantly affected by light treatment (Table 2).

250 3.1 Light-sensitive group responses

251 Dark interior sites supported higher light-sensitive species richness (Table 2), with no difference
252 between light edges and dark edges ($p > 0.05$). Similarly, dark interior sites supported the highest
253 light-sensitive bat activity (Table 2), but then dark edges supported higher activity than light edges
254 ($p = 0.037$, Table 2, Figure 3b). A similar pattern was seen for the most commonly recorded light-
255 sensitive species; *Vespadelus vulturnus* activity was highest at dark interior sites, lower at dark
256 edges, and lowest at light edges ($p = 0.02$, Table 2; Figure 3f). The activity of *Nyctophilus* spp. was
257 again highest at the dark interior sites, and significantly lower at both dark and light edges (Table
258 2). There was no significant difference between the *Nyctophilus* spp. activity at light and dark edges
259 ($p > 0.05$).

260 A higher proportion of the light-sensitive group's echolocation calls were recorded at the dark
261 edges than at the light edges, when compared with the proportion recorded at that site's dark
262 interior site ($F_{1,23} = 4.96$, $p = 0.038$; Figure 4). Where light-sensitive species were present, they were
263 more likely to be active at the edge if it was dark than if it was artificially lit.

264 3.2 Light-exploiting group responses

265 The species richness of the light-exploiting group was not affected by light treatment (Table 2).
266 Dark interior sites supported higher light-exploiting bat activity than light and dark edges (Table 2,

267 Figure 3c), and there was no difference between dark and light edges ($p > 0.05$). The activity of *C.*
268 *gouldii* followed a similar pattern, with activity highest at dark interior sites (Table 2, Figure 3d), with
269 no difference between light and dark edges ($p > 0.05$). However, the activity of *O. ridei* followed a
270 different pattern (Figure 3e); activity of this species was highest at light edges (Table 2, Figure 3e),
271 lower at dark edges, and lowest at dark interior sites ($p = 0.007$). There was no significant difference
272 in the proportion of the light-exploiting group's echolocation calls recorded at light edges and dark
273 edges, when compared with the proportion recorded at that site's dark interior site ($F_{1,2} = 1.08$, $p >$
274 0.05 ; Figure 4).

275 Habitat type, whether the forest was an isolated patch or connected to other forested areas, had no
276 significant effect on the activity or the species richness of the bat assemblage, the light-sensitive
277 group, or the light-exploiting group (Table 2).

278 3.3 Temporal activity patterns

279 Overall, there was no difference in first recording time between light treatments across species
280 (Table 3), however differences were found between functional groups.

281 The light-sensitive functional group was active significantly earlier at interior sites when compared
282 with dark and light edges (Table 3). There was no significant difference between the first recordings
283 at light and dark edges ($p > 0.05$). *Nyctophilus* spp. showed the same pattern (Table 3), again with
284 no difference between first recordings at light and dark edges ($p > 0.05$). There was no difference
285 between first recording times of *Vespadelus vulturnus* at both dark interior sites and dark edges
286 (Table 3). However, first recording time was significantly later at light edges than at dark interior
287 sites (Table 3) and dark edges ($p = 0.008$).

288 Overall, the first activity of the light-exploiting functional group was not significantly different
289 across light treatments (Table 3), but there were species-specific responses. First activity of the
290 light-exploiting *C. gouldii* was not significantly different across light treatments, however it was first

291 recorded significantly earlier in the night in connected forest than in patches (Table 3). Emergence
292 time in connected forest averaged 151.9 ± 9.1 minutes after sunset, versus 203.1 ± 16.9 minutes
293 after sunset in isolated forest patches. The time of first activity for *O. ridei* was significantly earlier at
294 dark interior sites than at both light and dark edges (Table 3). *O. ridei* was also recorded
295 significantly earlier at light edges than at dark edges ($p = 0.001$).

296 Throughout the night, the difference in the activity of the light-sensitive group between light and
297 dark edges was not as pronounced as the difference between interior sites and pooled edge sites.
298 The activity of the light-sensitive group was higher at interior sites throughout the night, and was at
299 its highest just after sunset (Figure 5).

300 3.4 Insect responses

301 Lepidoptera biomass was significantly affected by light treatment (Figure 3h); biomass was higher
302 at light edges than dark interior sites (Table 4) and posthoc tests showed that biomass at light
303 edges was higher than at dark edges also ($p < 0.001$). The average number of Lepidoptera caught at
304 dark interior sites did not differ from the number caught at dark edges (Table 4). However, the
305 number of Lepidoptera caught at light edges was significantly lower than dark interior sites (Table
306 4), and posthoc tests showed that the number of Lepidoptera at light edges was lower than at dark
307 edges also ($p = 0.012$).

308 4. Discussion

309 Our study demonstrates the disruptive effects of artificial light at the edges of urban forest on light-
310 sensitive and light-exploiting insectivorous bats. Our findings are consistent with research that
311 artificial light has a negative effect on certain species in ecologically sensitive habitat (Straka et al.
312 2016) and that artificial light at the urban forest edge contributes to a loss of functional connectivity
313 (LaPoint et al. 2015). Streetlights at the forest edge negatively affected the activity of the putative
314 light-sensitive group of bats. Sydney's smallest species, *V. vulturinus* was particularly negatively

315 affected by light, being less active and emerging later at artificially lit edges when compared with
316 dark edges. Despite light edges having greater vegetation cover with 250 m, bat activity and
317 richness was still lower here than at dark edges. Available functional habitat in urban forests is
318 reduced by artificial light, and with some species unable to cross lit areas (Hale et al. 2015), urban
319 biodiversity may continue to decline unless the degrading impacts of ALAN are addressed.

320 Species predicted to be light-exploiting were either unaffected by streetlights along the forest
321 edge, such as *C. gouldii*, or increased in activity, such as *O. ridei*. *Ozimops ridei* showed the strongest
322 positive response to artificial light at the forest edge, with higher activity and earlier emergence
323 time at artificially lit edges than dark edges, consistent with previous findings (Threlfall et al. 2013).
324 The species-specific differences within the *a priori* fast flying functional group suggest that
325 responses to ALAN may be more complex than basic guild-related responses. Our data implies that
326 other aspects of the urban environment may exert more influence on those species.

327 Whether the forest was connected to other forest or in an isolated patch, had little influence on the
328 effects of artificial light at the forest edge. *Chalinolobus gouldii* were recorded earlier in the night in
329 connected forest than in isolated patches, suggesting that as well as *C. gouldii* being unaffected by
330 artificial lights at the forest edge, this species may be more likely to roost in connected forest and
331 hence emerge earlier there. Our findings suggest that the bat assemblage appears relatively similar
332 across all forest habitat in this city, and this needs further investigation as it would inform urban
333 conservation strategy.

334 Recent multi-taxa research concluded that large connected patches of vegetation are critically
335 important for urban biodiversity (Beninde et al. 2015). Our data supports this, showing that total bat
336 activity, the activity of the light-sensitive species and *C. gouldii* were consistently higher on forest
337 interiors when compared with edges. *Nyctophilus gouldi* were rarely recorded anywhere but
338 bushland interiors, demonstrating the importance of forest interiors for bat diversity in cities.

339 With regards to insect trapping, Lepidoptera numbers were lowest at light edges, suggesting that
340 the biomass was made up of fewer but larger individuals. We conclude that our findings are
341 consistent with others (Pintérné and Pödör 2017), and may have been due to streetlights in the lit
342 conditions outshining our light traps, and attracting most of Lepidoptera away from the trap. In
343 future studies, suction traps (Shortall et al. 2009), sticky traps, malaise traps (Hosking 1979,
344 Hallmann et al. 2017) or camera traps (Rydell 1992) may be better alternatives for sampling
345 phototactic insects in artificially lit conditions.

346 4.1 Mechanisms driving light sensitivity in insectivorous bats

347 In line with our predictions, *V. vulturinus* was light sensitive, using forest edges less so when they were
348 lit. Thus ALAN may be contributing to edge effects and habitat loss for this species within cities
349 (Gonsalves and Law 2017). Of all *V. vulturinus* calls, 27 % were recorded at dark edges, and only 2 %
350 were recorded at artificially lit edges. This species was active significantly later at lit edges than at
351 dark edges. *Vespadelus vulturinus* is an edge-space foraging bat, although it is quite maneuverable
352 and so may not be as dependent on edges and flyways as other edge-space foraging bats (Law et al.
353 2011). *Vespadelus vulturinus* also flies closer to the ground in thinned as opposed to unthinned
354 understorey, perhaps for cover and protection (Adams 2012). Despite these flight preferences, our
355 data shows that this bat uses forest edges in cities, and is negatively impacted by light sources
356 along those edges. Its edge-space foraging preference makes *V. vulturinus*, and other slower-flying
357 edge-space foragers, susceptible to habitat loss and decline from streetlights at the forest edge.
358 This is consistent with previous research that failed to detect *V. vulturinus* in small pockets of urban
359 forest in highly urbanized parts of Sydney (Gonsalves and Law 2017).

360 In comparison, 92 % of calls identified as *Nyctophilus* spp., the species group adapted to foraging in
361 cluttered vegetation, were recorded at interior sites. Although *Nyctophilus* spp. have been observed
362 using open and edge habitat in woodland (Brigham et al. 1997), our study confirms low activity of
363 this species at the urban forest edge, regardless of whether streetlights were present or not.

364 Artificial light at the forest edge did not further reduced the low activity of *Nyctophilus* spp at these
365 locations. Our findings are consistent with a previous study that found that movements of these
366 taxa were mostly restricted within the bounds of an urban forest remnant (Threlfall et al. 2013).
367 These taxa appear to be light-sensitive (Threlfall et al. 2013), but the lack of edge habitat use
368 suggests both habitat fragmentation and disruption in the connectivity of dark vegetation across
369 cities have critically impacted the urban survival of this group. Some bats, including *Nyctophilus*
370 spp., could have retained a sensitivity to ultraviolet light (Gorresen et al. 2015), and this may cause
371 these species to avoid streetlights emitting ultraviolet, like the ones in this study.

372 *4.2 The importance of dark connected forest for urban bats*

373 Our study reveals that total bat activity was higher at dark interior sites than at either light or dark
374 forest edges, confirming previous research that dark forest is crucial for the persistence of some
375 insectivorous bats in cities (Threlfall et al. 2013, Hale et al. 2015, Straka et al. 2016, Azam et al.
376 2018), Haddock et al, in press). Activity at these dark forest interior sites peaks early in the night,
377 suggesting that this is where most bats roost in hollow trees. Throughout the course of the night,
378 the majority of calls were recorded at interior sites, whether looking at light-sensitive or light-
379 exploiting functional groups. Our findings provide support for the conservation of dark forest in
380 cities, and reconfirm the importance of connectivity between natural areas (Dearborn and Kark
381 2010, Goddard et al. 2010, Hale et al. 2012, Beninde et al. 2015), particularly dark corridors for light-
382 sensitive species (Bolívar-Cimé et al. 2013, Hale et al. 2015, Straka et al. 2016).

383 *4.3 Artificial light altering the competition for resources*

384 Niche differentiation between bat species can sometimes be subtle (Krüger et al. 2014) as bats
385 exploit slightly different insect prey in similar habitat. Clutter-adapted bats will glean moths and
386 beetles from the ground and from leaves, whereas open-space adapted bats will pursue prey on the
387 wing (Denzinger and Schnitzler 2013). Artificial light sources are known to attract insect prey out of
388 dark habitat and deplete foraging grounds for light-sensitive species (Rydell 1992, Rydell and Racey

389 1995, Arlettaz et al. 2000). Our data supports this effect, where overall moth biomass was
390 significantly higher at lit edges compared to dark edges and interior sites. Overall moth numbers
391 did not follow the same pattern, suggesting that larger insects dominated near streetlights. This
392 potential “vacuum cleaner effect”, where phototactic insects migrate out of dark forest and towards
393 artificial light, may be decreasing the amount of available prey to bats restricted to dark areas,
394 making it harder for them to persist in cities (Arlettaz et al. 2000). Investigation is needed into the
395 extent of this depletion of dark foraging grounds for light-sensitive bats. Our data shows that light-
396 sensitive bats are less likely to use artificially lit edges, and would therefore be less able to access
397 the increased insect biomass there. Similar to previous experiments, artificial light sources could be
398 creating foraging areas that mainly light-exploiting bats can exploit (Arlettaz et al. 2000, Stone et
399 al. 2015). ALAN, particularly artificial light sources at forest edges in cities, may be disrupting the
400 important environmental niches that allow bat species to co-exist.

401 *4.4 Light as an edge effect*

402 Artificial light as an edge effect has been studied in combination with traffic noise, mostly in the
403 context of road ecology. In this context it has strong negative effects on many nocturnal taxa
404 (Kempenaers et al. 2010, Hale et al. 2015, Azam et al. 2018). Mammal species richness increases at
405 the point where light levels return to ambient darkness, and bird diversity increases with distance
406 from the road (Pocock and Lawrence 2005). Small and narrow urban forest could be highly light-
407 impacted habitat (Azam et al. 2018). In our study, artificial light at the forest edge negatively
408 impacted species that may already be struggling to survive in cities. Functional diversity in
409 important urban forest patches and corridors may be significantly impacted, driven by an alteration
410 of the artificial lighting regime. Investigation into the zone of influence from permanent artificial
411 light sources on other taxa is a research priority.

412 *4.5 Lunar phobia and light phobia*

413 Light phobia could be driven by an innate lunar phobia, with changing moon phase and the
414 brightness of the moon linked to the emergence time and behaviour of some light-sensitive species
415 such as *V. vulturinus* and others (Law 1997, Saldaña-Vázquez and Munguía-Rosas 2013). Lunar
416 phobia is linked to morphological traits associated with foraging strategy; slow-flying bats respond
417 more negatively to bright moonlight (Saldaña-Vázquez and Munguía-Rosas 2013). These species
418 are also more likely to emerge later in the evening (Jones and Rydell 1994), theoretically because
419 they are adapted to hunting prey available in the darkest part of the night and so avoid crepuscular
420 predator peaks. Our data confirms this trend, that slow flying bat species avoid artificial light. This
421 morphological group may be responding negatively to artificial light as they have evolved to
422 respond negatively to moonlight. The species-specific differences here warrant further research.
423 Faster flying bats, those that appear more exploiting of artificial light, are less affected by
424 moonlight (Saldaña-Vázquez and Munguía-Rosas 2013). These species may be pre-adapted, or at
425 least resilient, to artificially lit environments. However much like the drivers of light phobia in bats,
426 the mechanisms driving lunar phobia are difficult to pinpoint. Periods of bright moonlight are
427 associated with reduced levels of insect prey (Lang et al. 2006), and may leave bats more vulnerable
428 to predation (Law 1997), particularly important for slow flying bats. Very few studies have provided
429 evidence that predation risk for bats increases under moonlit skies, even though it is discussed
430 frequently in the literature (Saldaña-Vázquez and Munguía-Rosas 2013, Stone et al. 2015). Future
431 studies teasing apart the causes of artificial light phobia, changes in food availability or predation
432 risk, would elucidate the mechanisms influencing lunar and light phobia in bats.

433 *4.6 Future directions and conclusions*

434 In urbanized Sydney, five species are at particular risk of ALAN degrading viable habitat. Elsewhere
435 the impact may be greater, for example; locations like tropical Barro Colorado Island in Panama are
436 home to a much higher proportion of slower flying bat species (Denzinger et al. 2017). If the
437 parameters of light sensitivity discussed here are applied to other bat communities, many more

438 species could be identified as at risk of habitat loss due to urban lighting at the edges of natural
439 forest. This is an issue for particular consideration in expanding cities and peri-urban areas. Lighting
440 near ecologically important areas, like drinking troughs, is already established as having a disruptive
441 effect on bat drinking behaviours (Russo et al. 2017, Russo et al. 2018). Foraging by many bats
442 species is affected also, and like others (Spoelstra et al. 2015, Straka et al. 2016), we recommend
443 avoiding the installation of streetlights near ecologically sensitive areas in cities, such as native
444 forests and wetlands. Other mitigation strategies, such as part night lighting, may be an alternative
445 to constant lighting (Azam et al. 2015); but need to be turned off early enough in the night to
446 successfully mitigate the impact on vulnerable species. If lighting near ecologically important forest
447 is necessary, red lights (usually between 620 and 750 nm) have been shown to have minimal effect
448 on a variety of mammal taxa (Spoelstra et al. 2015, Spoelstra et al. 2017), although their suitability
449 as a bat-friendly alternative is controversial (Voigt et al. 2018) and needs further testing. LED
450 technology allows lights to be manufactured to emit specific spectra, which has recently been found
451 to be useful for minimising disruption for bats (Haddock et al., in press). Research could be used to
452 help manufacturers create lights with the least disruptive spectra for nocturnal biodiversity.
453 However, conserving dark forested areas in cities remains crucial for the persistence of nocturnal
454 biodiversity such as light-sensitive insectivorous bats.

455

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459

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464

465

466 7. References

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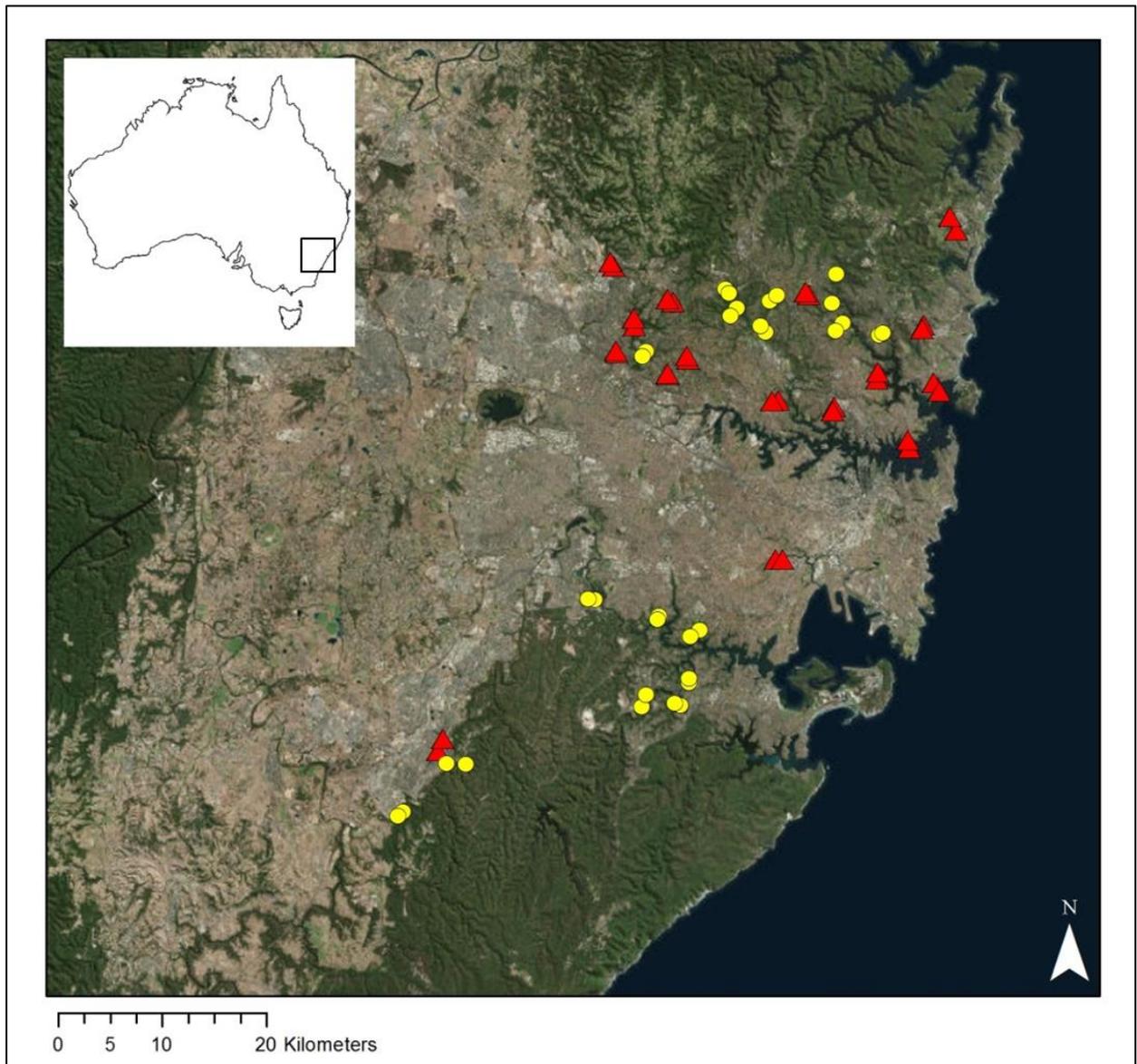
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Figure 1. Map showing location and distribution of forest patch sites (red triangles; n=15 pairs of control interior and edge sites) and connected forest sites (yellow circles; n=16 pairs of control interior and edge sites) relative to Sydney, Australia (inset).

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a)

b)



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719 Figure 2. Images taken from Google Earth of two of the sites in this study demonstrating the
 720 distinction between the patch and connected sites, with the green marker showing the position of
 721 the detector at the forest interior site and the blue marker showing the position of the detector at
 722 the forest edge site, a) Patch site: Cumberland State Forest, Sydney, b) Connected site: St Ives,
 723 Garigal National Park

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Table 1. All bat and insect response variables included in generalized linear mixed models

Category	Measurement	Response variable
BAT ACTIVITY	Average activity;	all bats the light-exploiting group <i>Chalinolobus gouldii</i> <i>Ozimops ridei</i> the light-sensitive group <i>Nyctophilus</i> spp. <i>Vespadelus vulturnus</i>
BAT SPECIES RICHNESS	Average species richness;	all bats for light-exploiting group for light-sensitive group
BAT EMERGENCE TIMES	Average time until first activity;	all bats for the light-exploiting group for the light-sensitive group

Chalinolobus gouldii

Ozimops ridei

Nyctophilus spp.

Vespadelus vulturnus

INSECT ABUNDANCE

Averages;

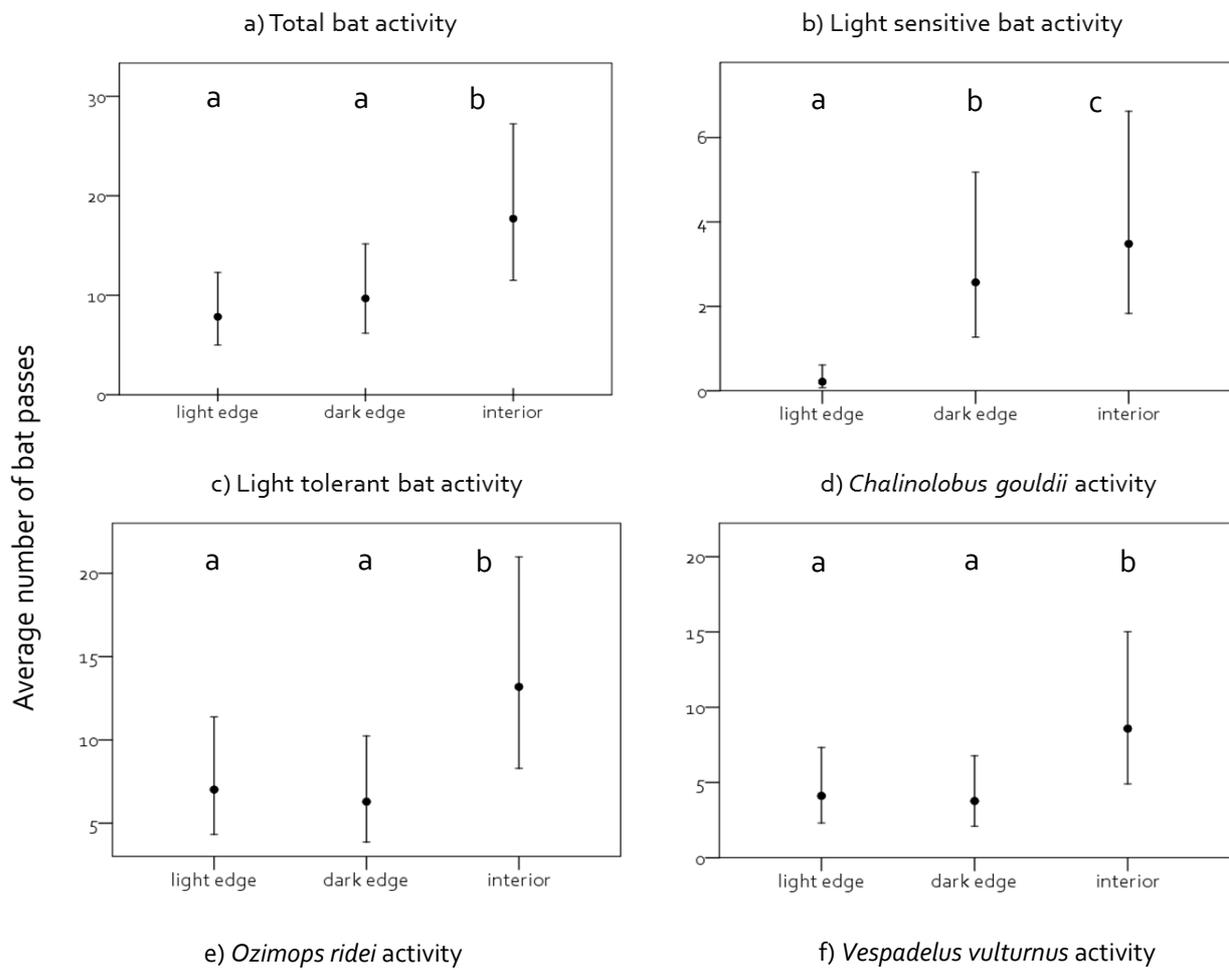
number of Lepidoptera collected

biomass of Lepidoptera

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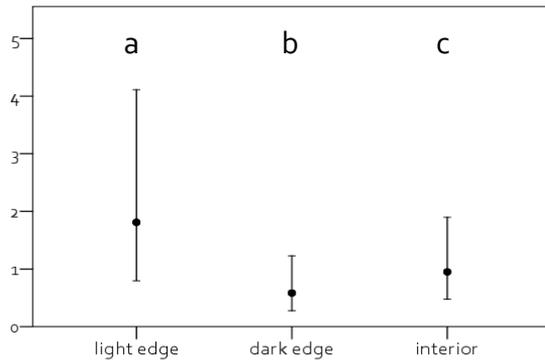
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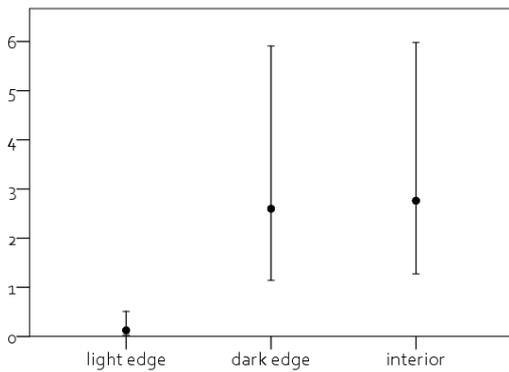
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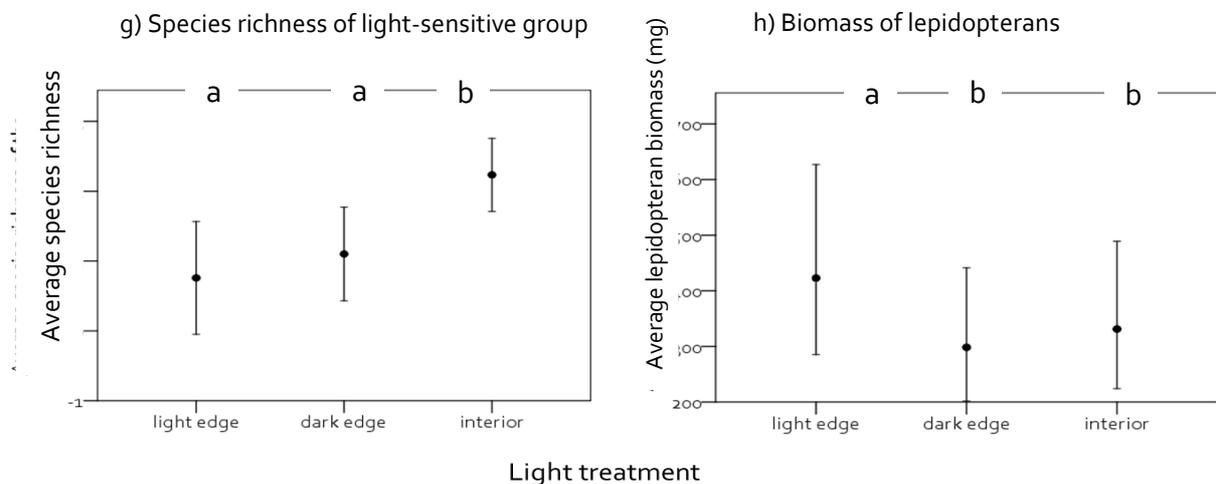
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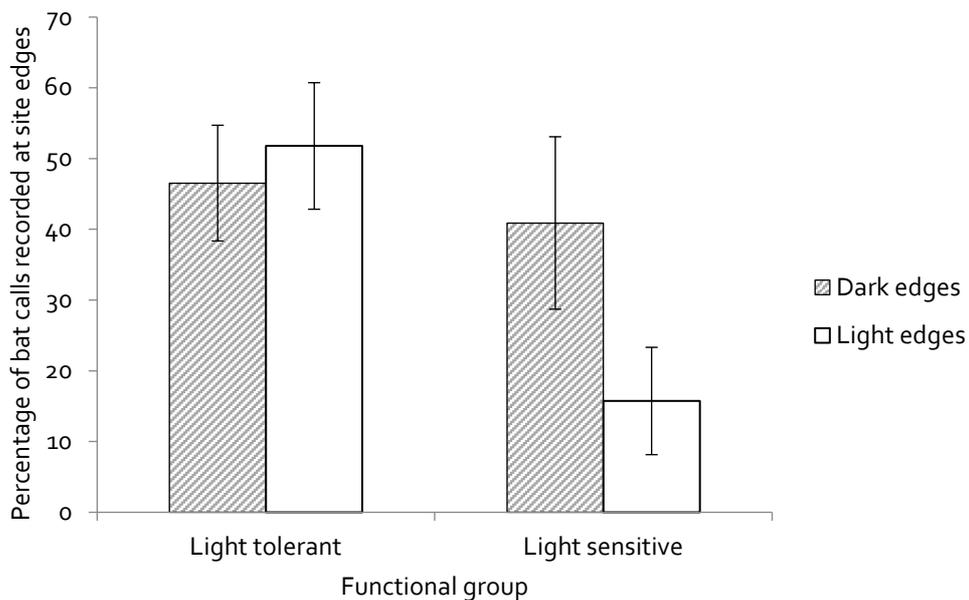
740 Figure 3. Plots showing marginal means (± 1 s.e.) after controlling for site. Figure 3a. Bat activity
 741 compared across light treatments; Figure 3b. Activity of the light-sensitive group compared across
 742 light treatments; Figure 3c. Activity of the light-exploiting group compared across light treatments;
 743 Figure 3d. Activity of *C. gouldii* compared across light treatments; Figure 3e. Activity of *O. ridei*
 744 compared across light treatments; Figure 3f. Activity of *V. vulturinus* compared across light
 745 treatments; Figure 3g. Species richness of the light-sensitive group compared across light
 746 treatments; Figure 3h. Lepidopteran biomass (mg) compared across light treatments. Statistically
 747 significant differences when comparing variable measurements between treatments are depicted
 748 using differing letters (a, b and c)

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751 Table 2. Results of GLMM with habitat type and light treatment as fixed effects, and site as a
 752 random effect, with response variables listed on the far left column, and the dark interior control
 753 treatment and patch treatment as the reference categories

Parameter	Estimate	Standard error	t value	p value
Total bat activity				
Intercept	2.834	0.3099	9.145	< 0.001
Connected forest versus patch	0.079	0.4288	0.185	0.854
Light edge versus interior	-0.814	0.0765	-10.642	< 0.001
Dark edge versus interior	-0.604	0.0791	-7.629	< 0.001
Average bat species richness				
Intercept	4.475	0.5258	8.511	< 0.001
Connected forest versus patch	0.330	0.6009	0.550	0.585
Light edge versus interior	-0.518	0.7435	-0.696	0.489
Dark edge versus interior	-0.577	0.7277	-0.793	0.431
Average light-sensitive species richness				
Intercept	2.256	0.3569	6.319	< 0.001
Connected forest versus patch	-0.044	0.3951	-0.112	0.911
Light edge versus interior	-1.475	0.4515	-3.268	0.002
Dark edge versus interior	-1.133	0.3953	-2.865	0.007
Average light-sensitive species activity				
Intercept	1.379	0.5022	2.745	0.009
Connected forest versus patch	-0.262	0.6275	-0.417	0.679
Light edge versus interior	-2.790	0.4203	-6.638	< 0.001
Dark edge versus interior	-0.305	0.1991	-1.531	0.134
Average <i>Nyctophilus</i> spp. activity				
Intercept	1.872	0.6269	2.985	0.005
Connected forest versus patch	-0.854	0.5699	-1.498	0.144
Light edge versus interior	-2.053	0.6654	-3.086	0.004

Dark edge versus interior	-1.540	0.5836	-2.639	0.013
<i>Average V. vulturnus</i> activity				
Intercept	1.282	0.6090	2.105	0.043
Connected forest versus patch	-0.533	0.7454	-0.714	0.480
Light edge versus interior	-3.100	0.5899	-5.256	< 0.001
Dark edge versus interior	-0.061	0.2235	-0.272	0.787
<i>Average light-exploiting species richness</i>				
Intercept	2.139	0.2016	10.610	< 0.001
Connected forest versus patch	-0.019	0.2304	-0.084	0.934
Light edge versus interior	0.338	0.2851	1.185	0.241
Dark edge versus interior	0.058	0.2790	0.208	0.836
<i>Average light-exploiting species activity</i>				
Intercept	2.581	0.3339	7.730	< 0.001
Connected forest versus patch	-0.004	0.4623	-0.008	0.994
Light edge versus interior	-0.630	0.0824	-7.653	< 0.001
Dark edge versus interior	-0.740	0.0902	-8.208	< 0.001
<i>Average C. gouldii</i> activity				
Intercept	2.214	0.4017	5.512	< 0.001
Connected forest versus patch	-0.130	0.5573	-0.232	0.817
Light edge versus interior	-0.736	0.0886	-8.308	< 0.001
Dark edge versus interior	-0.823	0.1071	-7.680	< 0.001
<i>Average O. ridei</i> activity				
Intercept	0.040	0.4916	0.082	0.935
Connected forest versus patch	-0.182	0.6445	-0.282	0.779
Light edge versus interior	0.644	0.3634	1.772	0.082
Dark edge versus interior	-0.489	0.1863	-2.626	0.011



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 757 Figure 4. Average percentage (\pm se) of light-sensitive and light-exploiting functional group
 758 echolocation calls recorded at light edge sites and at dark edge sites. Calculated by combining calls
 759 for each site with calls from associated interior control site and then calculating the percentage of
 760 the total calls recorded at the edge

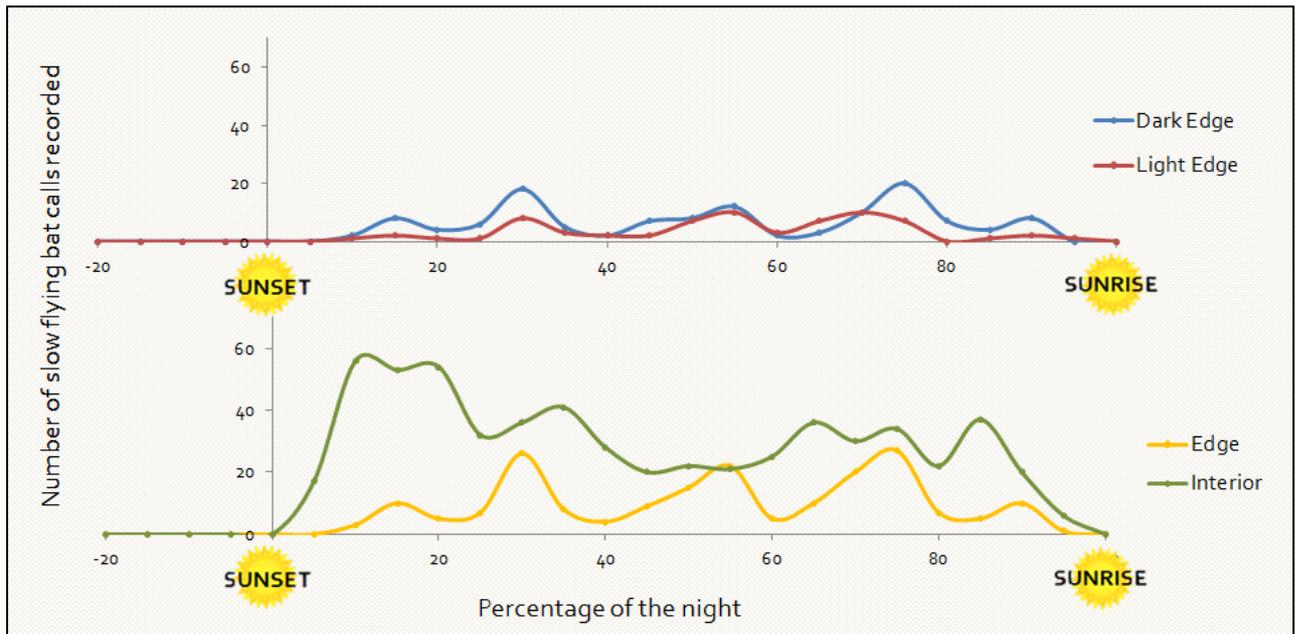
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 763 Table 3. Results of GLMM with habitat type and light treatment as fixed effects, and site as a
 764 random effect, with response variables listed on the far left column, and the dark interior control
 765 treatment and patch treatment as the reference categories

Parameter	Estimate	Standard error	t value	p value
Minutes until first bat activity				
Intercept	4.967	0.1635	30.383	< 0.001
Connected forest versus patch	-0.089	0.2312	-0.386	0.700
Light edge versus interior	-0.010	0.0289	-0.352	0.726
Dark edge versus interior	0.021	0.0278	0.744	0.460
Minutes until first light-sensitive group activity				
Intercept	5.386	0.1347	39.973	< 0.001
Connected forest versus patch	-0.013	0.1718	-0.077	0.939
Light edge versus interior	0.265	0.0397	6.687	< 0.001
Dark edge versus interior	0.232	0.0380	6.092	< 0.001

Minutes until first <i>Nyctophilus</i> spp. activity				
Intercept	5.500	0.1772	31.047	< 0.001
Connected forest versus patch	0.147	0.2225	0.659	0.518
Light edge versus interior	0.465	0.0615	7.563	< 0.001
Dark edge versus interior	0.462	0.0591	7.825	< 0.001
Minutes until first <i>V. vulturnus</i> activity				
Intercept	5.413	0.1748	30.962	< 0.001
Connected forest versus patch	0.151	0.2275	0.664	0.514
Light edge versus interior	0.252	0.0482	5.228	< 0.001
Dark edge versus interior	0.023	0.0559	0.411	0.685
Minutes until first light-exploiting group activity				
Intercept	5.064	0.0813	62.273	< 0.001
Connected forest versus patch	-0.045	0.1027	-0.442	0.660
Light edge versus interior	0.054	0.0974	0.557	0.580
Dark edge versus interior	0.050	0.0975	0.517	0.607
Minutes until first <i>C. gouldii</i> activity				
Intercept	202.150	16.7063	12.100	< 0.001
Connected forest versus patch	-53.183	20.6049	-2.581	0.013
Light edge versus interior	-15.014	23.1303	-0.649	0.519
Dark edge versus interior	26.846	24.3959	1.100	0.276
Minutes until first <i>O. ridei</i> activity				
Intercept	5.272	0.1409	37.419	< 0.001
Connected forest versus patch	-0.129	0.1919	-0.672	0.506
Light edge versus interior	0.176	0.0333	5.291	< 0.001
Dark edge versus interior	0.376	0.0419	8.961	< 0.001

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 769 Figure 5. Activity of light-sensitive bats throughout the night. This is calculated by noting sunset
 770 and sunrise each night of the survey and calculating what percentage of the night had elapsed when
 771 each call was recorded. The graph shows the number of calls recorded within each 10 percent
 772 increment throughout the night. The bottom graph shows the combined data from the edge sites
 773 compared with the data from the interior sites.

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 776 9. Appendix

777 *i Insect sampling*

778 Insects were sampled at the edge and interior locations of all patch sites (n = 30) for one night. For
 779 each patch, the edge and the interior were sampled on the same night to control for variation
 780 across nights. Sampling took place two weeks after acoustic sampling to avoid interfering with
 781 naturally occurring bat activity, however temperature and humidity were not significantly different
 782 and so insect sampling nights were deemed comparable to bat sampling nights. We avoided
 783 surveying on full moon and new moon nights, and for 3 days either side of both events. Black light
 784 intercept traps (Australian Entomological Supplies, Murwillumbah, Australia) were placed on the
 785 ground, in the same location used for the Anabat II detectors two weeks prior, less than 3 m from
 786 the base of the streetlight pole. 50ml of ethyl acetate was added to the bottom of the light trap,
 787 bulbs were attached to 12V batteries, and the trap was turned on between 2000 and 2300. Excalibur
 788 digital timers (Merlin Distribution, Roseville, Australia) automatically turned the lights off after 2

789 hours, and traps were collected within an hour of the light turning off. Individual insects were then
 790 separated and identified to order. Only Lepidoptera were included in the analysis as only a small
 791 number of insects of other orders, Dipterans and Coleopterans, were caught. Body length of each
 792 individual insects was measured, and biomass was calculated using established methods (Sample et
 793 al. 1993).

794 *ii Limitations of insect surveys*

795 Measurements of lepidopteran densities and biomass were counter-intuitive; firstly, biomass was
 796 higher at light edges than dark edges or interior control sites, consistent with previous research
 797 (Eisenbeis and Eick 2010, Barghini and Souza de Medeiros 2012, van Grunsven et al. 2014, Plummer
 798 et al. 2016). However secondly, Lepidoptera numbers were lowest at light edges, suggesting that
 799 the biomass was made up of fewer but larger individuals. For light-exploiting, larger aerial-hawking
 800 bats, moths attracted to artificially lit areas may therefore comprise an energy-rich food source of
 801 larger insect prey. Our result of lower numbers of moths around lights has been found in another
 802 study (Pintérné and Pödör 2017) , which found a higher number of lepidopteran in dark, semi-rural
 803 areas than in well-lit, urban areas. Our data may have been due to streetlights in the lit conditions
 804 outshining our light traps, and attracting most of Lepidoptera away from the trap (Pintérné and
 805 Pödör 2017). Although it seems illogical to sample the difference between light and dark conditions
 806 using an additional light source, this method is standard practice in studies of light (Spoelstra et al.
 807 2015, Pintérné and Pödör 2017).

808

809 Table 4. Results of GLMM with habitat type and light treatment as fixed effects, and site as a
 810 random effect, with response variables listed on the far left column, with patch and dark edge
 811 treatment as reference categories

Parameter	Estimate	Standard error	t value	p value
Biomass of Lepidoptera				
Intercept	5.731	0.0955	60.003	0.000

Connected forest versus patch	0.143	0.3798	0.375	0.710
Light edge versus interior	0.244	0.0309	7.896	0.000
Dark edge versus interior	-0.104	0.0262	-3.979	0.000
Average number of Lepidoptera caught				
Intercept	3.209	0.1598	20.080	0.000
Connected forest versus patch	-0.533	0.6323	-0.843	0.407
Light edge versus interior	-0.546	0.1289	-4.239	0.000
Dark edge versus interior	0.126	0.0845	1.495	0.146

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