

1 ***Haddock JK, Threlfall CG, Law B, et al. Responses of insectivorous bats and nocturnal***
2 ***insects to local changes in street light technology Austral Ecol (in press)***

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4 Responses of insectivorous bats and nocturnal insects to local changes in street light
5 technology

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16 Keywords

17 ALAN, artificial light, species traits, LED, mercury vapour, urban ecosystems

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19 Acknowledgements

20 Financial contributor: Holsworth Wildlife Research Endowment

21 This research has been approved by the Animal Ethics Committee at The University of
22 Sydney, protocol number 2015/786. This research is supported by the Australian

- 23 Government's National Environmental Science Program through the Clean Air and Urban
- 24 Landscapes Hub.
- 25

26 Abstract

27 Artificial light at night is a pervasive anthropogenic stressor for biodiversity. Many fast-
28 flying insectivorous bat species feed on insects that are attracted to lights emitting
29 ultraviolet radiation (10 nm to 400 nm). Several countries are currently focused on
30 replacing mercury vapour lamps, which emit ultraviolet light, with more cost efficient light
31 emitting diode (LED) lights, which emit less ultraviolet radiation. This reduction in
32 ultraviolet light may cause declines in insect densities in cities, predatory fast flying bats,
33 and in some edge foraging and slow flying bats. Capitalizing on a scheme to update
34 streetlights from high ultraviolet mercury vapour to low ultraviolet LED in Sydney,
35 Australia, we measured the activity of individual bat species, the activity of different
36 functional groups, and the bat and insect communities, before and after the change in
37 technology. We also surveyed sites already LED lights, sites with mercury vapour lights,
38 and unlit bushland remnants. Species adapted to foraging in cluttered vegetation, and
39 some edge-space foraging species, were more active in unlit bushland sites than in all lit
40 sites, and decreased in activity at lit sites after the change to LED lights. The change to LED
41 streetlights caused a decrease in the fast-flying *Chalinolobus gouldii* but not *Miniopterus*
42 *schreibersii oceanensis*, the latter being more influenced by seasonal and environmental
43 variables. Insect biomass was not affected by changing light types, but instead was
44 negatively correlated with the moon's percentage illuminance. Changing streetlights to
45 LEDs could result in a decline in some insectivorous bats in cities. This study confirms that
46 unlit urban bushland remnants are important refuges for high bat diversity, particularly for
47 more clutter-adapted species, and some edge-space foraging species. Preventing light
48 penetration in to unlit bushland patches and corridors remains essential to protect the
49 urban bat community.

50 Introduction

51 Seventy percent of the world's human population is predicted to be living in urban
52 settlements by 2050 (United Nations 2018) and cities are expanding to meet this demand
53 (Cohen 2003). Anthropogenic threats to biodiversity such as light, noise and air pollution,
54 and the fragmentation or degradation of natural habitat are at their most intense in cities
55 (Chan and Yao 2008, Hölker et al. 2010, Ortega 2012, Wolch et al. 2014). Despite this, urban
56 areas can support more threatened species than non-urban areas (Ives et al. 2016) and
57 therefore it is important to facilitate sustainable management for urban biodiversity.
58 Species rich urban ecosystems contribute to human wellbeing (Fuller et al. 2007, Taylor and
59 Hochuli 2015). Conservation of urban biodiversity requires an understanding of how
60 anthropogenic pressures are affecting remnant urban habitat and how to mitigate threats.

61 Artificial light at night (ALAN) is a rapidly growing global threat to biodiversity (Hölker et al.
62 2010) and is becoming more intense in cities (Falchi et al. 2016). Disruption to the natural
63 light/dark cycle, in terms of either light presence or spectra, can significantly alter urban
64 biodiversity (see Rich and Longcore 2013). Higher radiation of orange and red light can alter
65 plant growth and floral communities (Bennie et al. 2016), higher levels of ultraviolet light
66 can attract higher densities of insects (van Langevelde et al. 2011, Pawson and Bader 2014,
67 van Grunsven et al. 2014, Park and Lee 2017), and white light can decrease the utilization of
68 habitat by nocturnal mammals (Spoelstra et al. 2015). Residential areas in Sydney, Australia
69 rely almost entirely on white mercury vapour lighting, but many areas are now seeing
70 disruption in lighting technology with streetlights being replaced with more cost effective
71 and energy efficient LED technology (Ausgrid 2013), following a global trend. The new LED
72 lights emit white light in a similar high colour rendering index as mercury vapour lights,

73 both appearing white to human residents, but LED lights emit lower levels of ultraviolet
74 radiation (10 – 400nm), attract lower numbers of insects (van Grunsven et al. 2014), and are
75 generally brighter in lux than mercury vapour lights (Table 2). It remains a research priority
76 to understand the implications for biodiversity of these changes in urban lighting regimes.

77 Insectivorous bats commonly occur in cities (Van der Ree and McCarthy 2005, Jung and
78 Threlfall 2016), and for many species, their morphological and behavioural traits are
79 associated with different use of habitats (Avila-Flores and Fenton 2005, Denzinger and
80 Schnitzler 2013); the urban landscape represents a mosaic of different habitats for different
81 bat species. The responses of bat species to artificial light may also be linked to their
82 morphology and behaviour (Stone et al. 2015, Rowse et al. 2016). Faster flying bat species,
83 adapted to foraging and flying in open space (Neuweiler 1984), are most resilient to the
84 altered urban environment (Avila-Flores and Fenton 2005, Jung and Kalko 2011, Jung and
85 Threlfall 2016). Many of these species are able to use street lights as foraging grounds,
86 exploiting the increased abundance of insects that are attracted to the UV radiation
87 emitted by some street lights (Mathews et al. 2015, Stone et al. 2015, Rowse et al. 2016,
88 Lewanzik and Voigt 2017). Besides which, artificial light interferes with moth predator
89 evasion techniques, giving foraging bats an advantage over insect prey (Wakefield et al.
90 2015). An emerging global pattern is that ultraviolet-emitting street lights support higher
91 activity of faster flying bats, and if ultraviolet radiation is decreased, the fast flying bat
92 activity follows suit, probably tracking a decrease in ultraviolet-attracted insects (Lewanzik
93 and Voigt 2017). However, this pattern has not been established within the Australian bat
94 assemblage.

95 Not all species are able to exploit the 'night light niche' so successfully (Rich and Longcore
96 2013); many slower flying species adapted to cluttered vegetation (Neuweiler 1984) seem
97 to avoid lit areas (Stone et al. 2012, Bader et al. 2015, Jung and Threlfall 2016, Rowse et al.
98 2016) and remain in unlit bushland remnants (Threlfall et al. 2013). These slow flying
99 species are most at risk of local extinction (Jones et al. 2003), and so understanding their
100 response to different lighting types and spectra is a research priority. Stone et al. (2009)
101 found that LED lights set up along a hedgerow in the UK immediately excluded a
102 threatened species, *Rhinolophus hipposideros*, and another UK study confirmed that
103 lighting near a roost significantly disrupted colonies of slower flying, clutter-adapted bats
104 (Boldogh et al. 2007). This light avoidance could be due to their slower flight speed; these
105 slower flying species may not be as efficient at hunting flying insects that gather at light
106 sources (Neuweiler 1984) or may theoretically be less capable of evading predators that use
107 artificially lit areas as hunting grounds (Stone et al. 2015). If clutter adapted species are
108 recorded in artificially lit areas, it appears to be near lights that emit ultraviolet radiation
109 and presumably attract more insects (Stone et al. 2015, Rowse et al. 2016). *Myotis* spp. have
110 similar wing morphology to slow flying bats but may have retained a sensitivity to
111 ultraviolet light (Gorresen et al. 2015), and so avoid these lights; two major studies recorded
112 an increase in *Myotis* spp. after a change to low-ultraviolet LED lights (Rowse et al. 2016,
113 Lewanzik and Voigt 2017). Slower flying bats may be able to exploit insects at street lights,
114 but to a far lesser extent than faster flying species. However, we still do not fully
115 understand the impact that changing from mercury vapour to LED lights will have on
116 clutter-adapted, slow flying bats.

117 Species that forage along the edges of habitat, edge-space foragers (Neuweiler 1984), are
118 diverse in their echolocation call frequencies and flight patterns (Adams et al. 2005). They
119 are not known to respond in a uniform way to artificial light in an urban setting, although
120 edge-space foraging species that have high characteristic-frequency echolocation calls (the
121 frequency at the end of the flattest part of the call, ESH species, Table 1, (Law et al. 2002)
122 (Adams et al. 2005) are most reliant on denser, cluttered vegetation (Adams et al. 2009),
123 have shown the least positive response to artificial light in a forest setting when compared
124 with other edge-space foragers (Adams et al. 2005), and are known to respond differently
125 to different types of artificial lights (Jung and Kalko 2010). The impact of changing lighting
126 technology on this group has not been tested, though they share many traits with clutter-
127 adapted species and are sensitive to artificial light.

128 In this study, we had an opportunity to measure the local-scale, short term responses of the
129 bat assemblage and insect biomass to a change in light type from high-ultraviolet mercury
130 vapour lights to brighter LED lights, lower in ultraviolet radiation. We also surveyed the bat
131 assemblage at different light types and unlit bushland to assess how longer term
132 differences in spectra affected the bat assemblage and individual species.

133 We predicted the following responses;

134 1) That the urban bat and insect assemblages would respond to a change in light type from
135 mercury vapour to LED;

136 2) that the different light types would support different bat assemblages, with high-
137 ultraviolet mercury vapour lights supporting a higher abundance of insects, higher activity
138 of faster flying and higher activity of slow flying and ESH bats;

139 3) that unlit urban bushland would provide a refuge from artificial light for slow flying and
140 ESH bats.

141 Methods

142 Study site

143 The study was carried out in North Turramurra (Figure 1, coordinates 33°44'40.8"S
144 151°06'45.3"E), a leafy suburb of Sydney, Australia (Benson and Howell 1990), where bat
145 diversity is high (Basham et al. 2010). There are around 15 species found in the study area,
146 with diverse morphology and habitat requirements (Table 1). Sydney has high levels of
147 remnant native bushland abutting the urban matrix, however this habitat is rapidly
148 decreasing due to increased urbanization (Benson et al. 1995).

149 Experimental design

150 We surveyed four light treatments; sites being changed from mercury vapour to LED
151 technology (n = 2), sites with mercury vapour lights (n = 3, Figure 2a), sites with LED lights
152 (n = 3, Figure 2b), and unlit bushland (n = 3) which acted as reference sites. Sites were an
153 average of 1.55 kms (\pm s.e. 0.15 kms) apart, and therefore bat foraging activity at each site
154 was considered independent. We surveyed each site for an average of 8.3 nights (s.e. \pm
155 0.38) before the change in light type, and 9 nights (s.e. \pm 0.38) immediately after the
156 change in light type resulting in 192 detector recording nights (Table 2, Fischer et al. 2009).

157 We sampled between March and April of 2015, with the street lights being upgraded at the
158 changeover sites on the 10th March. The insectivorous bat population in this region can be
159 reliably measured at this time, as long bouts of hibernation mean the population can be
160 very low during winter months, and artificially high after December when the young begin
161 to fly (Churchill 2008).

162 Bat sampling

163 At each site, we used an Anabat II detector (Titley Electronics, Ballina, NSW Australia) with
164 the microphone 1 m above the ground and pointing upwards at a 45° angle to optimise the
165 amount of unobstructed airspace sampled and maximize sampling success (Law et al. 1998,
166 Patriquin et al. 2003, Threlfall et al. 2012). All detectors were calibrated to be equally
167 sensitive and were expected to detect a bat at 30 m, depending on species. At the lit sites
168 the detectors were placed a maximum of 3 m away from the base of the streetlight pointing
169 towards the light and along the road. At bushland sites, detectors were placed along
170 flyways; defined as pathways over 2 m in width with a break in the tree canopy. By ensuring
171 that the detectors at all sites were sampling habitat edges along the flyways or roads and
172 habitat interiors where present, we controlled as far as possible for differences in the bat
173 guilds present at different treatments. All recording nights had comparable weather
174 conditions (nights with rainfall over 3mm were excluded, average minimum daily
175 temperature per sampling period was between 16 and 18°C). The detectors pass the
176 information through a Zero-Crossings Interface Module (ZCAIM, Titley Electronics) and
177 divide the frequency of the echolocation recording by a constant factor, a division ratio, so
178 that the recording is audible to humans but retains all major characteristics of the call
179 needed for species identification (Corben 2004).

180 Processing of audio data

181 Recorded calls were identified using the AnaScheme and AnlookW software (Adams et al.
182 2010). For a bat call to be identified to species level, three or more pulses were required and
183 have characteristics that fall within the program's parameters for that species. A pass was
184 defined as at least three valid pulses with a minimum of 6 pixels per pulse. Positive species

185 identifications were made only when a minimum of 50% of pulses within a pass were
186 identified as the same species (Adams et al. 2009, Threlfall et al. 2012). The identification
187 key used in the analysis was developed for the Sydney area (Adams et al. 2010). The call
188 characteristics of *Nyctophilus gouldi* and *Nyctophilus geoffroyi* are indistinguishable using
189 the AnaScheme method and so were pooled as one taxon; *Nyctophilus* spp. The calls
190 identified as *Chalinolobus dwyeri*, *Falsistrellus tasmaniensis*, *Nyctophilus* spp., *Saccolaimus*
191 *flaviventris*, *Scoteanax rueppellii* and *Scotorepens orion* are known to be difficult to identify
192 and were checked manually to ensure conformance to other guides (Pennay et al. 2004,
193 Adams et al. 2010). In addition, calls were run through a filter in AnaScheme which is
194 specifically designed to identify alternating or unusual call characteristics of *Chalinolobus*
195 *gouldii* (B. Law, pers. comm., 2015). Only species that were positively identified using the
196 key, filters and manual checking were included for further analysis to eliminate any bias
197 caused by using partially identified species.

198 Assignment to a response group

199 To assess how traits influence responses to light and light changes we pooled activity data
200 for both slower flying species known to forage in cluttered environments preferentially, and
201 for species known to forage along the edges of habitat with higher characteristic-frequency
202 echolocation calls (Table 1, Norberg and Rayner 1987, Adams et al. 2005), in to one
203 response group. This included *Nyctophilus* spp., *Rhinolophus megaphyllus*, *Chalinolobus*
204 *morio*, *Miniopterus australis*, and *Vespadelus vulturnus*. We predicted a low detection rate
205 for these species at our artificially lit study sites and so pooled the species data to allow for
206 statistical analysis (Trindade-Filho et al. 2012) . We predicted that edge-space foraging
207 species with high (above 48 kHz) characteristic-frequency echolocation calls (ESH species,

208 Adams et al. 2009, Adams et al. 2005) and slow flying, clutter-adapted species may show a
209 similar response to a change in light type, and to artificially light generally (Stone et al.
210 2009, Threlfall et al. 2013, Lewanzik and Voigt 2017).

211 Insect sampling

212 Insects were sampled using 20x25cm white sticky traps (Bugs For Bugs Pty Ltd,
213 Mundubbera, Australia). Traps were deployed at every site at least twice before the change
214 in light type and a minimum of three times after the change in light type. Although it would
215 have been ideal to sample all sites on the same night, all trapping nights had comparable
216 weather conditions (no rainfall, minimum daily temperature between 16 and 18°C). Traps
217 were set up on wooden stakes at a height of 1.75m above the ground, opened within 30
218 minutes of sunset and collected within 40 minutes of sunrise. Sampling was conducted on
219 alternative nights to bat recording to avoid impacting bat behaviour. We identified insects
220 to order, and then measured the length of the insect and used algorithms (Sample et al.
221 1993) to estimate biomass. Over 91% of all insects caught were in the order Diptera, and so
222 other orders were excluded from further analysis.

223 Environmental variables

224 Daily minimum temperature (°C), rainfall (mm) and relative daily humidity (%) for all sites
225 were taken from the closest weather station (Parramatta North weather Station 066124,
226 Bureau of Meteorology). The percentage vegetation cover within a radius of 200 m was
227 calculated using Arc Map (ESRI, Redlands, USA, ver. 10.2) to be indicative of local
228 vegetation extent near the detector (Lacoeuilhe et al. 2014). Vegetation cover was
229 calculated by intersecting GPS points of our sites with the GIS layer 'The Native Vegetation

230 of the Sydney Metropolitan Area - Version 3, VIS_ID 4489' (NSW Office of Environment and
231 Heritage, Sydney). This vegetation layer is the most complete vegetation mapping for the
232 area and includes non-native vegetation. Light intensity (lux) and spectral outputs of the
233 different light types were measured using an l1Pro Spectrophotometer (X-rite, Melbourne,
234 Australia), with the spectrophotometer placed 1.5 m above the road surface directly below
235 the streetlight, or in the case of the bushland sites, 1.5 m directly above where the detector
236 was situated. One measurement per site was taken before and after the change in light
237 type. All light measurements were taken on a clear, new moon night between 2200 and
238 0000 hrs. Daily percentage of the moon illuminated was taken from the United States
239 Naval Oceanography Portal.

240 Statistical analysis

241 All analyses were carried out in SPSS (version 22, SPSS Inc., Chicago, USA). We defined
242 overall bat activity as the number of successfully identified passes recorded each night, the
243 activity of individual species as the number of successfully identified passes of that species
244 recorded each night, and the activity of response group species as the number of
245 successfully identified passes of that response group recorded each night. For each of the
246 11 sites we had two sampling periods, before and after the change in light type. The
247 number of recording nights during each sampling period ranged from 6 to 12 nights (Table
248 2) for bat recording, and between 2 and 4 nights for insect sampling (Table 2). Due to a non-
249 normal distribution, insect biomass was log transformed.

250 We used a general linear model (GLM) to compare the percentage vegetation cover
251 between light treatments, with a normal distribution and a log link function.

252 We wanted to elucidate if there were differences in lux from the different light treatments,
253 or from the change in light type. We performed a GLM with light treatment (mercury
254 vapour, LED, bushland and changeover), sampling periods (before and after the light
255 change), and the interaction included as fixed effects.

256 Insect biomass

257 To reduce factors in our model analyzing insect biomass data, we first used Pearson's
258 parametric bivariate correlation to assess the relationship between insect biomass and
259 weather variables (rainfall, temperature and percentage moon illumination and relative
260 humidity) measured on the corresponding day. As insect biomass was measured on fewer
261 days than bat activity, these tests have lower degrees of freedom (Table 3). The percentage
262 of the moon illuminated was the only influential factor ($p < 0.05$), so it was retained and
263 included in that GLMM. We aimed to establish if insect biomass differed between light
264 treatments, and before and after the change in light type by using a generalized linear
265 mixed model. In this GLMM light treatment (mercury vapour, LED, bushland or
266 changeover), sampling period (before or after the light change), the interaction between
267 the two, and the percentage of the moon illuminated were fixed effects, and site was a
268 random effect to account for repeated measurements. For all GLMMs we used a Poisson
269 distribution with a log link function. Fisher's Least Significant Difference was used as a post
270 hoc test.

271 Bat and insect activity analysis

272 We used Pearson's parametric bivariate correlation to assess the relationships between
273 daily bat activity measures (activity of all bats, *C. gouldii*, *M. schreibersii oceanensis* and

274 clutter-adapted/ESH response group) and daily weather variables (rainfall, temperature and
275 percentage moon illumination and relative humidity), to avoid overparameterization and
276 reduce variables in our models. This revealed that relative humidity was the only influential
277 factor ($p < 0.05$) when considering bat activity, *C. gouldii* activity and *M. schreibersii*
278 *oceanensis* activity, and so it was included in further generalized linear mixed models
279 (GLMMs) for those response variables. Percentage moon illumination was significantly
280 correlated with the activity of the clutter-adapted/ESH response group and so was included
281 in that GLMM.

282 We aimed to understand if the change in light type caused a change in the bat assemblage,
283 and to understand the relative importance of unlit bushland as refuge habitat compared
284 with other light treatments, by conducting a series of GLMMs. Our response variables were
285 overall bat activity, the activity of *C. gouldii*, the activity of *M. schreibersii oceanensis*, and
286 the pooled activity of the clutter-adapted/ESH response group. For all GLMMs we used a
287 Poisson distribution with a log link function. Light treatment (mercury vapour, LED,
288 bushland or changeover), sampling period (before and after the light change) and the
289 interaction between the two were included as fixed effects. We also included either relative
290 humidity or percentage moon illuminated as fixed effects, as described above. We included
291 site as a random effect to account for repeated measures at the same site. For the light
292 treatment fixed effect, we set the reference category as the bushland treatment, for the
293 before/after fixed effect, we set the reference category as the before treatment. Fisher's
294 Least Significant Difference was used as a post hoc test.

295 To assess compositional differences in the bat communities between light treatments, we
296 used PRIMER (version 7, Quest Research, New Zealand). We standardised samples and

297 then used a fourth root transformation as our bat activity data was skewed. We then
298 generated a Bray-Curtis similarity matrix from transformed activity data for all species, due
299 to non-normal distribution that violated assumptions. From the transformed dataset, we
300 conducted a similarity percentage analysis (SIMPER) and a permutational multivariate
301 analysis of variance (PERMANOVA).

302 Results

303 We detected 14 different bat species at our study sites. Five of these are listed as vulnerable
304 (Table 1, NSW Biodiversity Conservation Act 2016). We successfully identified 6118 calls to
305 species or species group, and this was 56.5% of all calls detected (typical of studies from
306 Sydney (Threlfall et al. 2011)). These 14 species compose 77% of the bat species known to
307 occur in the area (Basham et al. 2010, Threlfall et al. 2011). Species we did not detect,
308 *Myotis macropus*, *Mormopterus norfolkensis* and *Chalinolobus dwyeri*, are all known to be
309 either rare or reliant on caves or water bodies, and so it was deemed that further sampling
310 would not have detected these species.

311 Environmental variables across light treatments

312 The average percentage vegetation within a 200m radius significantly differed between
313 light treatments ($F_{(3,10)} = 4.37$, $p = 0.049$, Table 4), with bushland sites having the highest
314 amount of vegetation compared with sites with LED lights, sites with mercury vapour lights
315 and changeover sites.

316 Lux differed between light treatments ($F_{(3,14)} = 53.5$, $p < 0.001$), with bushland being the
317 darkest ($n = 2$, mean = 0.47, compared with LED lights ($n = 2$, mean = 15, se = 0.97), mercury
318 vapour lights ($n = 2$, mean = 10.3, se = 0.78) or at changeover sites ($n = 2$, mean = 12.45, se =

319 1.45). Post hoc tests also showed that lux did not change significantly at the changeover
320 sites after the change in light type ($p > 0.05$), but lux did differ significantly between
321 mercury vapour and LED treatments ($p = 0.002$).

322 Insect biomass, light treatments and percentage moon illuminated

323 Insect biomass was unaffected by light treatment ($F_{(3,20)} = 0.68, p > 0.05$) and the
324 interaction between light treatment and sampling period (before and after the change in
325 light type) was also not significant ($F_{(3,20)} = 2.18, p > 0.05$). Insect biomass was significantly
326 affected by the percentage of the moon illuminated ($F_{(3,20)} = 8.17, p < 0.001$).

327 Activity of *Chalinolobus gouldii* between treatments

328 Of the 6118 calls identified to species or species level, 62.8% were *C. gouldii*. This species
329 was significantly affected by relative humidity ($F_{(3,183)} = 320.67, p < 0.001$) and the
330 interaction effect was significant ($F_{(3,183)} = 320.67, p < 0.001$). Post hoc comparisons showed
331 that *C. gouldii* activity at the changeover sites and at bushland sites was higher before when
332 compared after the change in light (Table 3). At mercury vapour and LED lit sites, *C. gouldii*
333 activity was lower before the change in light type and then increased after the change
334 (Table 3).

335 Activity of *Miniopterus schreibersii oceanensis* across treatments

336 Identified calls of this species made up 11.8% of all identified calls. This species was
337 significantly affected by relative humidity ($F_{(1,183)} = 49.24, p < 0.001$) and the interaction
338 was significant ($F_{(1,183)} = 12.75, p < 0.001$). Post hoc comparisons showed that *M. schreibersii*
339 *oceanensis* activity at changeover sites and bushland sites was lower before the change in
340 light type (Table 3) and then increased. *Miniopterus schreibersii oceanensis* activity at

341 mercury vapour sites was higher before the change in light type, and then decreased after
342 the change (Table 3).

343 Clutter-adapted and ESH bats

344 Bats categorised as within our response group, slow flying and ESH species, were rarely
345 detected, making up only 2.05 % of all identified calls. The activity of this functional group
346 significantly differed across light treatments ($F_{(2,183)} = 14.03$, $p < 0.001$), with unlit bushland
347 supporting higher activity (Table 3). The activity of the clutter-adapted/ESH response group
348 was significantly affected by the percentage moon illuminated ($F_{(1,183)} = 9.42$, $p = 0.002$).

349 The interaction between light treatment and before/after the change in light type was
350 significant (Figure 3, $F_{(2,183)} = 5.49$, $p = 0.024$), with activity remaining consistent at all light
351 treatments except for the changeover sites, where activity significantly decreased (Table 3).

352 Differences in bat communities between light treatments

353 Composition of bat communities was not significantly different before and after the change
354 in light type at the changeover sites (Figure 4, pseudo $F_{4,21} = 1.5$, $p = 0.672$). When
355 comparing light treatments (pooled across the before and after the light change groups),
356 bat communities in bushland habitat were significantly different to mercury vapour sites
357 (Figure 4, pseudo $F_{4,21} = 2.08$, $p = 0.036$) and different to LED sites (Figure 4, pseudo $F_{4,21} =$
358 2.23 , $p = 0.022$). These differences were driven by both the higher activity of faster flying
359 species, *C. gouldii* and *M. schreibersii oceanensis*, at the lit sites, and the absence of the
360 slower flying, clutter-adapted species group *Nyctophilus* spp. from any of the lit sites.

361 Discussion

362 Our results show that changing street lights from mercury vapour to LED decreased the
363 activity of our response group, including species adapted to cluttered vegetation and
364 species adapted to edges of habitat with relatively high-frequency echolocation calls. This
365 decrease in clutter-adapted and ESH bat activity was related to the installation of LED
366 street lights and potentially a decrease in UV radiation. Our data provides evidence that
367 clutter-adapted/ESH species may exploit the ultraviolet-attracted insect prey to some
368 extent, but activity declines when the light type is changed to LED lights, supporting similar
369 findings by Stone et al (2015).

370 Unlit urban bushland as refuge for high urban bat diversity

371 The bat community in the urban bushland significantly differed from the community in the
372 urban matrix; fast flying species such as *C. gouldii* and *M. schreibersii oceanensis* dominated
373 the lit areas of the urban matrix, while the clutter-adapted/ESH response group was
374 significantly more active in unlit bushland remnants. Our results confirm that changing to
375 LED street lights causes at least a short term decrease in clutter-adapted/ESH species, and
376 that unlit bushland is important habitat. The activity of the clutter-adapted/ESH response
377 group (*Nyctophilus* spp., *Rhinolophus megaphyllus*, *Vespadelus vulturnus*, *Chalinolobus morio*
378 and *Miniopterus australis*) was significantly higher in unlit bushland sites. We did not have
379 an opportunity to survey unlit streets as a procedural control in this experiment, and so we
380 are unable to state that these bats were avoiding artificial light or whether this effect is due
381 to habitat preference. Edge-space foraging and clutter-adapted species are positively
382 influenced by vegetation density (Threlfall et al. 2013, Suarez-Rubio et al. 2018). From
383 previous research (Threlfall et al. 2013) and our findings, it is apparent that artificial lighting
384 as well as vegetation density plays a role in habitat preference for bats, but further work is

385 needed to disentangle the two driving factors. However, unlit urban bushland seems to be
386 important for the persistence of both slower flying, clutter-adapted bats and edge-space
387 foraging species with higher characteristic-frequency echolocation calls. Slower flying,
388 clutter-adapted bats may have evolved to emerge in the darkest part of the night (Jones
389 and Rydell 1994) and to specialize in hunting insects in cluttered vegetation, along habitat
390 edges, and in small unlit open spaces (Brigham et al. 1997). We support Rydell's (1992)
391 suggestion that slow flight and a gleaning foraging strategy may be morphological
392 constraints, rendering these species less able either to exploit insects around street lights
393 (Jones and Rydell 1994, Rydell et al. 1996) or to evade visual predators that may use lit
394 urban areas as hunting grounds (Speakman 1991), although direct evidence for the latter is
395 still lacking. Slower flying, clutter-adapted species are most at risk of extinction (Jones et al.
396 2003, Safi and Kerth 2004) due to rapid habitat fragmentation and destruction, and are at
397 significant risk from increased artificial light pollution. Our findings also highlight however,
398 that edge-spaced foraging species with high characteristic-frequency echolocation calls
399 may also be negatively affected by changing to LED lights and a loss of unlit habitat.
400 Further research is needed to disentangle the importance of habitat type and artificial light
401 levels for these species and understand species-specific responses, as this group may be at
402 risk of increasing light pollution in cities.

403 Bat responses to different light types and light changes

404 Our data suggest that different street light types do not support significantly different
405 overall bat assemblages. Contrary to our predictions and previous research (Rowse et al.
406 2016, Lewanzik and Voigt 2017), mercury vapour street lights high in UV radiation did not
407 support higher overall bat activity, higher activity of faster flying bats or higher insect

408 biomass than low UV LED street lights. However, changing the light type at a site caused
409 some immediate species- and group-specific responses within the bat assemblage. We
410 measured a decrease in the activity of clutter-adapted/ESH response group after the
411 installation of low-UV LED lights. This decrease in activity did not mirror the availability of
412 insect prey we recorded however, which did not respond to the change to LED lights.
413 However, insect biomass was negatively correlated with the percentage of the moon
414 illuminated over the course of this experiment (Bishop et al. 2000, Guimarães et al. 2000).
415 Whatever was driving the change in insect biomass, this provides evidence that neither *C.*
416 *gouldii*, *M. schreibersii oceanensis* nor the clutter-adapted/ESH group activity were tracking
417 insect availability as none showed the same activity patterns as the insects. The bats may
418 be responding to something other than a change in insect biomass; perhaps instead the
419 increased intensity of the LED lights or a change in insect species composition.

420 Activity of *M. schreibersii oceanensis* increased in the second half of the experiment, and
421 particularly at changeover sites and bushland sites. This species is known to migrate out of
422 Sydney to maternity colonies in the summer months (Gonsalves and Law 2017), and return
423 in autumn. The increased activity that we recorded across all light treatments may be
424 attributed to adults and juveniles returning to the city following the autumn dispersal
425 (Dwyer 1963). Further, the increases in *M. schreibersii oceanensis* activity at both the
426 changeover sites after the lights changed to LED, and the bushland sites, suggest that this
427 species is not influenced by light type but is influenced by wider landscape variables that we
428 did not measure in this experiment, like proximity to an appropriate subterranean roost.

429 Recommendations for urban planning and future research

430 This study highlights the importance of protecting bushland remnants as refuges for
431 clutter-adapted and ESH bats. Small remnants (<40 ha) have a positive conservation value
432 for highly light avoidant species (Threlfall et al. 2012, Threlfall et al. 2013), but protecting
433 their low ambient light levels may be important for more bat species to forage and
434 commute. We do not know the impact of artificial lighting on the quality of remaining
435 bushland patches. Penetration of light into bushland edges is known to alter mammal,
436 vegetation and bird diversity (Pocock and Lawrence 2005). Future work should focus on the
437 effect of light penetration into remnant patches, including narrow corridors, for clutter
438 adapted and ESH species, and devise ways to maximize the conservation value of this
439 remaining habitat with ecologically sensitive public lighting policies. Research should
440 assess long term and city-wide surveys after spectra changes in streetlights. Time
441 constraints and the staggered nature of the installation of LED street lights across Sydney
442 meant that we could only survey a limited number of sites where lights were being
443 changed. Future research could focus on longer-term studies that examine many different
444 changeovers at various times. It remains a priority to partner with relevant government
445 stakeholders and installation companies to conduct studies investigating the impact of
446 lighting on nocturnal fauna when entire neighborhoods have their street lights changed.
447 Longer term surveying, both before and after changes in lighting, could also uncover long
448 term patterns that were undetectable in this study. For cities to conserve high nocturnal
449 species diversity, the conservation of unlit urban bushland should be considered a research
450 and planning priority, and considered when designing street light upgrade projects.

451 All data is available from the authors on request.

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