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

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31 Abstract

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

more clutter-adapted species, and some edge-space foraging species. Preventing light penetration in to unlit bushland patches and corridors remains essential to protect the urban bat community.

Introduction

Seventy percent of the world's human population is predicted to be living in urban settlements by 2050 (United Nations 2018) and cities are expanding to meet this demand (Cohen 2003). Anthropogenic threats to biodiversity such as light, noise and air pollution, and the fragmentation or degradation of natural habitat are at their most intense in cities (Chan and Yao 2008, Hölker et al. 2010, Ortega 2012, Wolch et al. 2014). Despite this, urban areas can support more threatened species than non-urban areas (Ives et al. 2016) and therefore it is important to facilitate sustainable management for urban biodiversity. Species rich urban ecosystems contribute to human wellbeing (Fuller et al. 2007, Taylor and Hochuli 2015). Conservation of urban biodiversity requires an understanding of how anthropogenic pressures are affecting remnant urban habitat and how to mitigate threats. Artificial light at night (ALAN) is a rapidly growing global threat to biodiversity (Hölker et al. 2010) and is becoming more intense in cities (Falchi et al. 2016). Disruption to the natural light/dark cycle, in terms of either light presence or spectra, can significantly alter urban biodiversity (see Rich and Longcore 2013). Higher radiation of orange and red light can alter plant growth and floral communities (Bennie et al. 2016), higher levels of ultraviolet light can attract higher densities of insects (van Langevelde et al. 2011, Pawson and Bader 2014, van Grunsven et al. 2014, Park and Lee 2017), and white light can decrease the utilization of habitat by nocturnal mammals (Spoelstra et al. 2015). Residential areas in Sydney, Australia rely almost entirely on white mercury vapour lighting, but many areas are now seeing disruption in lighting technology with streetlights being replaced with more cost effective and energy efficient LED technology (Ausgrid 2013), following a global trend. The new LED lights emit white light in a similar high colour rendering index as mercury vapour lights, both appearing white to human residents, but LED lights emit lower levels of ultraviolet radiation (10 – 400nm), attract lower numbers of insects (van Grunsven et al. 2014), and are generally brighter in lux than mercury vapour lights (Table 2). It remains a research priority to understand the implications for biodiversity of these changes in urban lighting regimes.

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

Not all species are able to exploit the 'night light niche' so successfully (Rich and Longcore 2013); many slower flying species adapted to cluttered vegetation (Neuweiler 1984) seem to avoid lit areas (Stone et al. 2012, Bader et al. 2015, Jung and Threlfall 2016, Rowse et al. 2016) and remain in unlit bushland remnants (Threlfall et al. 2013). These slow flying species are most at risk of local extinction (Jones et al. 2003), and so understanding their response to different lighting types and spectra is a research priority. Stone et al. (2009) found that LED lights set up along a hedgerow in the UK immediately excluded a threatened species, *Rhinolophus hipposideros*, and another UK study confirmed that lighting near a roost significantly disrupted colonies of slower flying, clutter-adapted bats (Boldogh et al. 2007). This light avoidance could be due to their slower flight speed; these slower flying species may not be as efficient at hunting flying insects that gather at light sources (Neuweiler 1984) or may theoretically be less capable of evading predators that use artificially lit areas as hunting grounds (Stone et al. 2015). If clutter adapted species are

recorded in artificially lit areas, it appears to be near lights that emit ultraviolet radiation and presumably attract more insects (Stone et al. 2015, Rowse et al. 2016). *Myotis* spp. have similar wing morphology to slow flying bats but may have retained a sensitivity to ultraviolet light (Gorresen et al. 2015), and so avoid these lights; two major studies recorded an increase in *Myotis* spp. after a change to low-ultraviolet LED lights (Rowse et al. 2016, Lewanzik and Voigt 2017). Slower flying bats may be able to exploit insects at street lights, but to a far lesser extent than faster flying species. However, we still do not fully understand the impact that changing from mercury vapour to LED lights will have on clutter-adapted, slow flying bats.

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

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

We predicted the following responses;

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

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

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

Methods

Study site

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

Experimental design

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

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

Bat sampling

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

Processing of audio data

Recorded calls were identified using the AnaScheme and AnalookW software (Adams et al. 2010). For a bat call to be identified to species level, three or more pulses were required and have characteristics that fall within the program's parameters for that species. A pass was defined as at least three valid pulses with a minimum of 6 pixels per pulse. Positive species identifications were made only when a minimum of 50% of pulses within a pass were identified as the same species (Adams et al. 2009, Threlfall et al. 2012). The identification key used in the analysis was developed for the Sydney area (Adams et al. 2010). The call characteristics of *Nyctophilus gouldi* and *Nyctophilus geoffroyi* are indistinguishable using the AnaScheme method and so were pooled as one taxon; *Nyctophilus* spp. The calls identified as *Chalinolobus dwyeri*, *Falsistrellus tasmaniensis*, *Nyctophilus* spp., *Saccolaimus flaviventris*, *Scoteanax rueppellii* and *Scotorepens orion* are known to be difficult to identify and were checked manually to ensure conformance to other guides (Pennay et al. 2004, Adams et al. 2010). In addition, calls were run through a filter in AnaScheme which is

specifically designed to identify alternating or unusual call characteristics of *Chalinolobus gouldii* (B. Law, pers. comm., 2015). Only species that were positively identified using the key, filters and manual checking were included for further analysis to eliminate any bias caused by using partially identified species.

Assignment to a response group

To assess how traits influence responses to light and light changes we pooled activity data for both slower flying species known to forage in cluttered environments preferentially, and for species known to forage along the edges of habitat with higher characteristic-frequency echolocation calls (Table 1, Norberg and Rayner 1987, Adams et al. 2005), in to one response group. This included *Nyctophilus* spp., *Rhinolophus megaphyllus*, *Chalinolobus morio*, *Miniopterus australis*, and *Vespadelus vulturnus*. We predicted a low detection rate for these species at our artificially lit study sites and so pooled the species data to allow for statistical analysis (Trindade-Filho et al. 2012) . We predicted that edge-space foraging species with high (above 48 kHz) characteristic-frequency echolocation calls (ESH species, Adams et al. 2009, Adams et al. 2005) and slow flying, clutter-adapted species may show a similar response to a change in light type, and to artificially light generally (Stone et al. 2009, Threlfall et al. 2013, Lewanzik and Voigt 2017).

Insect sampling

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

228 Environmental variables

229 Daily minimum temperature (°C), rainfall (mm) and relative daily humidity (%) for all sites
230 were taken from the closest weather station (Parramatta North weather Station 066124,
231 Bureau of Meteorology). The percentage vegetation cover within a radius of 200 m was
232 calculated using Arc Map (ESRI, Redlands, USA, ver. 10.2) to be indicative of local
233 vegetation extent near the detector (Lacoeuilhe et al. 2014). Vegetation cover was
234 calculated by intersecting GPS points of our sites with the GIS layer 'The Native Vegetation
235 of the Sydney Metropolitan Area - Version 3, VIS_ID 4489' (NSW Office of Environment and
236 Heritage, Sydney). This vegetation layer is the most complete vegetation mapping for the
237 area and includes non-native vegetation. Light intensity (lux) and spectral outputs of the
238 different light types were measured using an l1Pro Spectrophotometer (X-rite, Melbourne,
239 Australia), with the spectrophotometer placed 1.5 m above the road surface directly below
240 the streetlight, or in the case of the bushland sites, 1.5 m directly above where the detector
241 was situated. One measurement per site was taken before and after the change in light
242 type. All light measurements were taken on a clear, new moon night between 2200 and
243 0000 hrs. Daily percentage of the moon illuminated was taken from the United States
244 Naval Oceanography Portal.

245 Statistical analysis

246 All analyses were carried out in SPSS (version 22, SPSS Inc., Chicago, USA). We defined
247 overall bat activity as the number of successfully identified passes recorded each night, the
248 activity of individual species as the number of successfully identified passes of that species
249 recorded each night, and the activity of response group species as the number of
250 successfully identified passes of that response group recorded each night. For each of the
251 11 sites we had two sampling periods, before and after the change in light type. The
252 number of recording nights during each sampling period ranged from 6 to 12 nights (Table
253 2) for bat recording, and between 2 and 4 nights for insect sampling (Table 2). Due to a non-
254 normal distribution, insect biomass was log transformed.

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

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

Insect biomass

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

Bat and insect activity analysis

We used Pearson's parametric bivariate correlation to assess the relationships between daily bat activity measures (activity of all bats, *C. gouldii*, *M. schreibersii oceanensis* and clutter-adapted/ESH response group) and daily weather variables (rainfall, temperature and percentage moon illumination and relative humidity), to avoid overparameterization and reduce variables in our models. This revealed that relative humidity was the only influential factor ($p < 0.05$) when considering bat activity, *C. gouldii* activity and *M. schreibersii oceanensis* activity, and so it was included in further generalized linear mixed models (GLMMs) for those response variables. Percentage moon illumination was significantly correlated with the activity of the clutter-adapted/ESH response group and so was included in that GLMM.

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

To assess compositional differences in the bat communities between light treatments, we used PRIMER (version 7, Quest Research, New Zealand). We standardised samples and then used a fourth root transformation as our bat activity data was skewed. We then generated a Bray-Curtis similarity matrix from transformed activity data for all species, due to non-normal distribution that violated assumptions. From the transformed dataset, we conducted a similarity percentage analysis (SIMPER) and a permutational multivariate analysis of variance (PERMANOVA).

Results

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

Environmental variables across light treatments

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

Lux differed between light treatments ($F_{(3,14)} = 53.5$, $p < 0.001$), with bushland being the darkest ($n = 2$, mean = 0.47, compared with LED lights ($n = 2$, mean = 15, se = 0.97), mercury vapour lights ($n = 2$, mean = 10.3, se = 0.78) or at changeover sites ($n = 2$, mean = 12.45, se = 1.45). Post hoc tests also showed that lux did not change significantly at the changeover sites after the change in light type ($p > 0.05$), but lux did differ significantly between mercury vapour and LED treatments ($p = 0.002$).

Insect biomass, light treatments and percentage moon illuminated

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

Activity of *Chalinolobus gouldii* between treatments

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

Activity of *Miniopterus schreibersii oceanensis* across treatments

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

light type (Table 3) and then increased. *Miniopterus schreibersii oceanensis* activity at mercury vapour sites was higher before the change in light type, and then decreased after the change (Table 3).

Clutter-adapted and ESH bats

Bats categorised as within our response group, slow flying and ESH species, were rarely detected, making up only 2.05 % of all identified calls. The activity of this functional group significantly differed across light treatments ($F_{(2,183)} = 14.03$, $p < 0.001$), with unlit bushland supporting higher activity (Table 3). The activity of the clutter-adapted/ESH response group was significantly affected by the percentage moon illuminated ($F_{(1,183)} = 9.42$, $p = 0.002$). The interaction between light treatment and before/after the change in light type was significant (Figure 3, $F_{(2,183)} = 5.49$, $p = 0.024$), with activity remaining consistent at all light treatments except for the changeover sites, where activity significantly decreased (Table 3).

Differences in bat communities between light treatments

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

Discussion

Our results show that changing street lights from mercury vapour to LED decreased the activity of our response group, including species adapted to cluttered vegetation and species adapted to edges of habitat with relatively high-frequency echolocation calls. This decrease in clutter-adapted and ESH bat activity was related to the installation of LED street lights and potentially a decrease in UV radiation. Our data provides evidence that clutter-adapted/ESH species may exploit the ultraviolet-attracted insect prey to some

extent, but activity declines when the light type is changed to LED lights, supporting similar findings by Stone et al (2015).

Unlit urban bushland as refuge for high urban bat diversity

The bat community in the urban bushland significantly differed from the community in the urban matrix; fast flying species such as *C. gouldii* and *M. schreibersii oceanensis* dominated the lit areas of the urban matrix, while the clutter-adapted/ESH response group was significantly more active in unlit bushland remnants. Our results confirm that changing to LED street lights causes at least a short term decrease in clutter-adapted/ESH species, and that unlit bushland is important habitat. The activity of the clutter-adapted/ESH response group (*Nyctophilus* spp., *Rhinolophus megaphyllus*, *Vespadelus vulturnus*, *Chalinolobus morio* and *Miniopterus australis*) was significantly higher in unlit bushland sites. We did not have an opportunity to survey unlit streets as a procedural control in this experiment, and so we are unable to state that these bats were avoiding artificial light or whether this effect is due to habitat preference. Edge-space foraging and clutter-adapted species are positively influenced by vegetation density (Threlfall et al. 2013, Suarez-Rubio et al. 2018). From previous research (Threlfall et al. 2013) and our findings, it is apparent that artificial lighting as well as vegetation density plays a role in habitat preference for bats, but further work is needed to disentangle the two driving factors. However, unlit urban bushland seems to be important for the persistence of both slower flying, clutter-adapted bats and edge-space foraging species with higher characteristic-frequency echolocation calls. Slower flying, clutter-adapted bats may have evolved to emerge in the darkest part of the night (Jones and Rydell 1994) and to specialize in hunting insects in cluttered vegetation, along habitat edges, and in small unlit open spaces (Brigham et al. 1997). We support Rydell's (1992) suggestion that slow flight and a gleaning foraging strategy may be morphological constraints, rendering these species less able either to exploit insects around street lights (Jones and Rydell 1994, Rydell et al. 1996) or to evade visual predators that may use lit urban areas as hunting grounds (Speakman 1991), although direct evidence for the latter is still lacking. Slower flying, clutter-adapted species are most at risk of extinction (Jones et al. 2003, Safi and Kerth 2004) due to rapid habitat fragmentation and destruction, and are at significant risk from increased artificial light pollution. Our findings also highlight however, that edge-spaced foraging species with high characteristic-frequency echolocation calls

may also be negatively affected by changing to LED lights and a loss of unlit habitat. Further research is needed to disentangle the importance of habitat type and artificial light levels for these species and understand species-specific responses, as this group may be at risk of increasing light pollution in cities.

Bat responses to different light types and light changes

Our data suggest that different street light types do not support significantly different overall bat assemblages. Contrary to our predictions and previous research (Rowse et al. 2016, Lewanzik and Voigt 2017), mercury vapour street lights high in UV radiation did not support higher overall bat activity, higher activity of faster flying bats or higher insect biomass than low UV LED street lights. However, changing the light type at a site caused some immediate species- and group-specific responses within the bat assemblage. We measured a decrease in the activity of clutter-adapted/ESH response group after the installation of low-UV LED lights. This decrease in activity did not mirror the availability of insect prey we recorded however, which did not respond to the change to LED lights. However, insect biomass was negatively correlated with the percentage of the moon illuminated over the course of this experiment (Bishop et al. 2000, Guimarães et al. 2000). Whatever was driving the change in insect biomass, this provides evidence that neither *C. gouldii*, *M. schreibersii oceanensis* nor the clutter-adapted/ESH group activity were tracking insect availability as none showed the same activity patterns as the insects. The bats may be responding to something other than a change in insect biomass; perhaps instead the increased intensity of the LED lights or a change in insect species composition.

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

Recommendations for urban planning and future research

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

All data is available from the authors on request.

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Table 1. Functional group assignment for predicted response to artificial light, based on previous classifications, physical attributes and known flight patterns

Species name	Call description and characteristic frequency (CF) * & ^	Foraging area ** & ^^	Foraging guild ***	Wing loading^^^	Aspect ratio^^^	Putative light sensitive group
<i>Chalinolobus gouldii</i>	Curved, alternating, 28 – 31 kHz CF	Edge	ESL	8.20 ± 2.26	6.53 ± 0.41	
<i>Falsistrellus tasmaniensis</i> *^	Curved and steep, 35 – 39.5 kHz CF	Edge	ESM			
<i>Miniopterus schreibersii oceanensis</i> *^	Curved, down-sweeping tail, 43 – 47 kHz CF	Edge	ESM	9.71 ± 1.59	6.66 ± 0.28	
<i>Mormopterus ridei</i>	Flat, 28.5 – 31 kHz CF	Open	OS			
<i>Austronomus australis</i>	Flat or curved, 10 – 13 kHz CF	Open	OS	15.46 ± 1.71	7.99 ± 0.45	
<i>Saccolaimus flaviventris</i> *^	Curved, 18 – 21.5 kHz CF		OS	15.90 ± 2.47	8.25 ± 0.42	
<i>Scoteanax rueppellii</i> *^	Curved, 33 – 36 kHz CF	Edge	ESL	12.56 ± 0.22	6.36 ± 0.27	
<i>Scotorepens orion</i>	Curved, 34 – 37 kHz CF	Edge	ESL	10.43 ± 1.59	5.97 ± 0.54	
<i>Vespadelus darlingtoni</i>	Curved, 42 – 45 kHz CF	Edge	ESM			
<i>Chalinolobus morio</i>	Curved, down-sweeping tail, 47.5 – 53 kHz CF	Edge	ESH	6.29 ± 1.08	6.11 ± 0.31	Light sensitive
<i>Miniopterus australis</i> *^	Curved, down-sweeping tail, 57 – 63 kHz CF	Edge	ESH	5.77 ± 1.32	6.79 ± 0.48	Light sensitive
<i>Vespadelus vulturinus</i>	Curved, up-sweeping tail, 49 – 54 kHz CF	Edge	ESH	6.36 ± 0.53	5.19 ± 0.54	Light sensitive
<i>Nyctophilus gouldi</i>	Near vertical, starts 70/80 kHz dropping to 35/45 kHz CF	Clutter	CA	6.20 ± 1.25	5.46 ± 0.30	Light sensitive
<i>Nyctophilus geoffroyi</i>	Near vertical, starts 70/80 kHz dropping to 35/45 kHz CF	Clutter	CA	5.91 ± 0.97	5.60 ± 0.55	Light sensitive

<i>Rhinolophus megaphyllus</i>	Flat, 66 – 72 kHz CF	Clutter	CA	6.77 ± 1.05	4.98 ± 1.05	Light sensitive
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* = Reinhold et al. (2001) ^ = Pennay et al. (2004) ** = Adams et al. (2009) *** = Adams et al. (2005) ^^ = Milne et al. (2004) ^^ = Rhodes (2002) *^ = Conservation status: VULNERABLE (NSW Biodiversity Conservation Act 2016)

Table 2. Sampling intensity at all sites, both before and after the change in light type at sites 1 and 2, along with ambient light measures and streetlight type

Site Number	Treatment	Light intensity (lux) on clear, full moon night	Bat sampling intensity (detector nights)		Insect sampling intensity (trapping nights)	
			Before	After	Before	After
Site 1	80W Mercury Vapour changed to 29W LED	13 lux changed to 15 lux	7	8	2	3
Site 2	80W Mercury Vapour changed to 29W LED	8.3 lux changed to 13 lux	6	12	2	2
Site 3	80W Mercury Vapour	7.9 lux	8	8	2	3
Site 4	80W Mercury Vapour	12 lux	10	10	2	2
Site 5	80W Mercury Vapour	11 lux	8	9	2	2
Site 6	Bushland	0.47 lux	8	8	2	3
Site 7	Bushland	0.66 lux	10	8	2	2
Site 8	Bushland	0.29 lux	8	9	2	2
Site 9	29W LED	16 lux	8	8	2	3
Site 10	29W LED	12 lux	10	12	2	2
Site 11	29W LED	17 lux	8	9	2	2

Table 3. Pairwise contrasts for each generalised linear mixed model, including coefficients and confidence intervals, with 'after' as the reference category, where a positive contrast estimate indicates a decrease in the response variable from before to after the change in light type, and a negative contrast estimate indicates an increase in the response variable

Model term	Light	Pairwise Contrast	Contrast				Adj.	95% Confidence Interval	
	Treatment		Estimate	Std. Error	t	df	Sig.	Lower	Upper
<i>Chalinolobus gouldii</i>	changeover	before versus after	2.598	.107	24.302	183	< 0.001	2.387	2.809
	MV	before versus after	-0.987	.074	-13.369	183	< 0.001	-1.133	-0.842
	bushland	before versus after	0.907	.074	12.301	183	< 0.001	.761	1.052
	led	before versus after	-0.428	.077	-5.519	183	< 0.001	-0.581	-0.275
<i>Miniopterus schreibersii oceanensis</i>	changeover	before versus after	-1.874	0.305	-6.150	183	< 0.001	-2.475	-1.273
	MV	before versus after	-0.996	0.133	-7.481	183	< 0.001	-1.258	-0.733
	bushland	before versus after	1.133	0.197	5.758	183	< 0.001	0.744	1.521
	led	before versus after	-0.125	0.284	-0.441	183	0.660	-0.685	0.435
Light sensitive bats	changeover	before versus after	1.869	0.691	2.704	182	0.008	0.505	-3.232
	MV	before versus after	-0.342	0.791	-0.432	182	0.666	-1.902	1.218
	bushland	before versus after	-0.903	0.551	-1.640	182	0.103	-1.990	0.184
	led	before versus after	-0.707	0.551	1.283	182	0.201	-1.794	-0.380
Insect biomass	changeover	before versus after	0.660	1.777	-0.371	20	0.714	-4.367	-3.047
	MV	before versus after	-1.276	0.964	-1.324	20	0.201	-3.287	0.735
	bushland	before versus after	-2.099	1.265	-1.659	20	0.113	-4.738	0.540

Table 4. Descriptive statistics of all response variables, within each light treatment, and before and after the change in light type

	Light treatment	Before			After		
		N (number of replicate nights)	Mean	Standard deviation	N (number of replicate nights)	Mean	Standard deviation
<i>Chalinolobus gouldii</i> activity (average number of passes per night)	Bushland	26	32.54	55.06	26	10.92	14.72
	Changeover	13	75.08	88.10	20	5.05	6.30
	LED	25	11.80	14.59	29	14.52	19.58
	MV	25	11.04	10.34	28	22.93	32.80
<i>Miniopterus schreibersii oceanensis</i> activity (average number of passes per night)	Bushland	26	3.27	7.41	26	1.65	2.42
	Changeover	13	0.92	1.66	20	6.80	7.78
	LED	25	0.80	1.50	29	1.24	1.64
	MV	25	3.24	2.52	28	10.96	12.19
Clutter-adapted and ESH species activity (average number of passes per night)	Bushland	26	1.81	4.60	26	2.12	3.65
	Changeover	13	1.08	1.89	20	0.10	0.31
	LED	25	0	0	29	0	0
	MV	25	0.20	0.50	28	0.11	0.31
Insect biomass (average biomass in grams)	Bushland	6	0.50	4.57	7	5.07	0.50
	Changeover	4	0.50	0.74	5	1.33	0.33
	LED	6	2.28	1.88	7	2.24	1.89
	MV	6	0.85	1.65	7	3.07	0.24
Percentage vegetation cover (m ²)	Bushland	3	52.10	0.86			
	Changeover	2	56.06	15.24			
	LED	3	87.36	14.89			

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63. - \$%//%&&8#4/'3/', '/&>'0'?\$%32 \$%39@ %4'A= 0&=30: '+</4&BCD', /%&&8#4/'3/', '/&EF"0'G=2 +&9@ %4'A= 0&=)

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3, , &2 +3#&3/'/4&+\$, 480: ', /&, ': "58& '%/- '/4&1- 2 . - , /"- 0'- 5/4&+3/'3, , &2 +3#&'0'/4&8/'2 3/%R, "/&, 'X "/4'3' (D', /%&, '
- 5F)E>J'G "0/, '%& %&, 80/'4&+3/'3, , &2 +3#&5 %&314', "/&&/'4&%+85 %&- %35&%4&1430#&'0'8#4/'/= . &)J430#&- 68%& '
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J430#&- 68%& 'X4&, - 8: '+8&/'%30#&, <%& %&, 80/, '/4&+3/'3, , &2 +3#&3/'1430#&- 68%&/'&, '35&%4&1430#&'0'8#4/'/= . &)
K &1\$%&'63. - \$%&/'&, '3&%& %&, 80/& '+="06&%& %&: '/%30#&, 9+\$, 480: ', /&, '3&%& %&, 80/& '+=#%&80', S\$3%&, 930: 'BCD'
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