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

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Abstract

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

1. Introduction

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

Providing “stepping stones and corridors” of forests and native vegetation is a commonly suggested
conservation action for urban biodiversity (Dearborn and Kark 2010, Beninde et al. 2015).
Connecting forest habitat in cities can mitigate species loss and biotic homogenisation
(Lindenmayer and Nix 1993, Fischer and Lindenmayer 2007) by facilitating movement (Dearborn
and Kark 2010) and genetic diversity (Aguilar et al. 2008) of native animals across a degraded urban
landscape. Over the last few decades, research has focused on quantifying the characteristics of
habitat remnants that maximize their value to native plants and animals, including their size (Evans
et al. 2009), shape (Hawrot and Niemi 1996), and connectedness (Keitt et al. 1997, McGarigal et al.
2002, Beninde et al. 2015). Calculating the amount of viable habitat existing in urban areas is a more
complex process. It must incorporate not only structural elements of forest areas, such as their size
and shape, but also functional connectivity (Kupfer 2012), and whether structural habitat features
are actually used. Anthropogenic pressures, such as ALAN, may impact functional connectivity
(Hale et al. 2012) by narrowing wildlife corridors and reducing functional patch sizes, however, the extent to which this occurs is poorly understood currently.

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

Dark habitats are currently at risk from the edge effects of ALAN.

Insectivorous bats are an ecologically diverse group, and respond in a variety of ways to urbanisation (Russo and Ancillotto 2015). Some faster flying open-space adapted bat species find roosts in buildings (Kunz 1982) and can commute across urbanised landscapes (Jung and Kalko 2011). Conversely, other slower flying clutter-adapted bat species commonly avoid urban areas, they cannot adapt to changes in roost availability and instead are reliant on networks of urban forest to survive in cities (Basham et al. 2011). Artificial light is one anthropogenic pressure driving these diverse responses to urban areas. Ultraviolet radiation attracts high numbers of insects (van Grunsven et al. 2014) and could offer urban feeding grounds for faster flying bat species adapted to exploit this resource (Rydell 1992, Rydell and Racey 1995). These bats may be able to dive through the light cone when foraging (Blake et al. 1994) and perhaps able to evade any aerial predators that use the lit areas as hunting grounds. Conversely, slower flying clutter-adapted species often avoid artificially lit areas (Stone et al. 2012) and may be constrained by lights at the patch edge, spending...
a majority of their foraging time within dark patches (Threlfall et al. 2013, Hale et al. 2015), and therefore reducing their functional urban habitat. Artificial light also markedly delays some species’ emergence times from roosts (Jones and Rydell 1994, Downs et al. 2003, Boldogh et al. 2007), meaning that their foraging time is reduced and the health of the population may at risk (Boldogh et al. 2007). There is a global pattern emerging that ALAN negatively affects species adapted to foraging in either cluttered vegetation or along habitat edges, like *Rhinolophus hipposideros* (Stone et al. 2012), *Eptesicus serotinus* (Azam et al. 2018), and *Nyctophilus gouldi* (Threlfall et al. 2013). The mechanistic drivers of this light phobia in bats are not completely understood (Stone et al. 2015, Rowse et al. 2016) but could include predator avoidance (Speakman 1991, Stone et al. 2009, Lima and O’Keefe 2013), morphology that leaves slower flying bats less able to exploit airborne insect prey at lights compared with faster flying bats like *Pipistrellus pipistrellus* (Haffner and Stutz 1985) sensitivity to ultraviolet radiation emitted by some streetlights (Gorresen et al. 2015), or a combination of these. Bats with many of these traits are declining in cities (Jung and Threlfall 2016, Jung and Threlfall 2018) hence research on the impact of public lighting on this group is urgently required.

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

2. Method

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

2.2 Experimental design

We conducted an acoustic survey along 31 forest edge sites (Figure 1); 16 of these sites were at the edges of connected forest (forest connected to large natural areas, Figure 2a), and 15 were on the edges of isolated forest patches (Figure 2b), >30 ha in size, but surrounded on all sides by urban matrix. Of all connected patch edge sites, half the sites (n=7) had 80W mercury vapour streetlights along the edges (light intensity of 10.65 lux ± 1.89) and half of the sites (n=8) were dark (light intensity of 0.52 lux ± 0.34). Of all forest patch edge sites, half the sites (n=8) had 80W mercury vapour streetlights along the edges (light intensity of 10.20 lux ± 1.23) and half of the sites (n=8) were dark (light intensity of 0.97 lux ± 0.52). All edge sites were defined as roads or pathways over 4m in width with dense vegetation on only one side. Dark edges were defined as 30m of uninterrupted dark conditions (artificial light levels comparable to ambient darkness and no external light sources on nearby houses). Artificially lit edges were defined as 30m of 80W mercury vapour lights along one side of the road, with the streetlights at a median distance apart of 12.1m. Usual low-level urban lighting from houses in the surrounding matrix was present at both dark and light edges. We additionally located control sites in the dark interior of all 31 sites (lux of 0.55 ± 0.20), which were located along an internal edge comprising a pathway or track (2 m typical width) between 400 m and 1 km perpendicular from the sampled forest edge. This allowed us to sample
the bat assemblage at 31 edge sites, and 31 dark interior control sites, leading to 62 sites in total. We sampled between November and December of 2016, the maternity season for bats when resource requirements and activity levels are highest. The light intensity (lux) at each site was measured using a lux meter (QM1587; Reduction Revolutions Pty Ltd, Parramatta, Australia). We also measured insect biomass at all forest patches, at both the interior and edge site, using a black light intercept traps (Australian Entomological Supplies, Murwillumbah, Australia, see Appendix)

2.3 Bat recording

The acoustic survey was carried out using Anabat II detectors (Titley Electronics, Ballina, Australia) placed on the ground with the high frequency microphone positioned 1 m above the ground and pointing upwards at a 45° angle to record all echolocation calls of passing bats. We used one detector per site, and predicted to still record high flying bats to be recorded due to louder calls from those species (Jung and Kalko 2011). At artificially lit edges the detector was placed no further than 3 m from the base of the streetlight pole, no more than 3 m away from the edge of the forest. At both the edge and interior sites, the microphone was pointed parallel down the forest edge and down the interior track or path, respectively, to optimise the amount of habitat sampled (Law et al. 1998, Threlfall et al. 2012). Each of the 62 sites were sampled between 3 – 5 consecutive nights (average 4.35 nights ± s.e. 0.19, due to unexpected equipment failure we did not manage to record for 5 nights at each site), totaling 270 recording nights across the entire survey. A maximum of eight sites were surveyed on the same night, where the edge and its respective interior control were concurrently sampled. The detectors passed the data through a Zero-Crossings Interface Module (ZCAIM; Titley Electronics). The acoustic files collected during the survey were processed using Anascheme and a bat call identification key developed for Sydney bats (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. Successful 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 calls identified as *Chalinolobus dwyeri, Falsistrellus tasmaniensis, Nyctophilus* spp., *Saccolaimus flaviventris, Scotaneex rueppellii* and *Scotorepens orion* are known to be complex or rare and were manually checked against known parameters and confirmed or re-identified (Adams et al. 2010). In addition, calls were run through a species filter in AnaScheme which is specifically designed to identify calls of *Chalinolobus gouldii* with alternating frequency. The call characteristics of *Nyctophilus gouldi* and *Nyctophilus geoffroyi* are indistinguishable using the AnaScheme method and so were pooled as one taxon; *Nyctophilus* spp. 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.

2.4 Assignment to functional groups

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

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

2.6 Statistical analysis

All analyses were carried out in SPSS (version 22, SPSS Inc., Chicago, USA). For each of the 31 sites and their dark interior urban forest controls, average activity and total species richness was calculated for the bat assemblage, for the light-exploiting functional group, for the light-sensitive functional group and for each individual species. Average activity was calculated by summing the total number of identified passes detected at that site during the recording time, and then dividing by the number of sampling nights at that site. Total species richness was calculated by counting the number of species detected at that site over the recording time. To calculate the time until first activity, and therefore potential delay or disturbance to the bats, we located the earliest call for a functional group or species at a particular site and then subtracted that time from the time of sunset that day (EST), leaving the numbers of minutes after sunset that the call was recorded. When discussing the comparison of a response variable across light treatments, we are including light edges, dark edges and dark interiors.
Generalized linear models (GLMs) were used to establish statistical differences in both lux level and vegetation extent between the three light treatments, with the habitat treatment (connected or patch) and light treatment (light edge or dark edge) as fixed effects.

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

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

We used Poisson distribution models with a log link function and robust variance estimates for all but two of the GLMMs as the data did not follow a normal distribution (Yau and Kuk 2002), the exceptions were light-sensitive bat activity and *Nyctophilus* spp. activity. Light-sensitive bat activity was low across all treatments and so a negative binomial distribution with a log link function with robust variance estimates was used in the GLMM. Soft-calling *Nyctophilus* spp. were recorded in
such low numbers that activity of this taxa was converted to presence-absence data, and a GLMM was run using a binomial distribution with a probit link function, again with robust variance estimates. All post hoc tests were Fisher’s Least Significant Difference.

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

3. Results

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

Artificially lit edges, dark edges and interiors all differed significantly from each other in the amount of vegetation cover within 250 m of each site. Interior control sites had greater vegetation extent than dark edges (p < 0.005), and light edges had greater vegetation extent than dark edges (p < 0.05). Forest patches had significantly less vegetation cover within a 250 m radius of each site than connected forest (p < 0.001). Artificially lit edges were significantly brighter ($F_{4,59} = 157.9$, p<0.005) than dark edges (p < 0.005) and dark interiors (p < 0.005).
Echolocation calls of bats were recorded at all sites. Light-exploiting bat species were detected at 95% of sites; with 96% of edge sites and 93% of interior sites. Light-sensitive bat species were detected at 51% of sites, including 41% of edge sites, and 61% at interior sites.

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

3.1 Light-sensitive group responses

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

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

3.2 Light-exploiting group responses

The species richness of the light-exploiting group was not affected by light treatment (Table 2).

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

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

### 3.3 Temporal activity patterns

Overall, there was no difference in first recording time between light treatments across species (Table 3), however differences were found between functional groups. The light-sensitive functional group was active significantly earlier at interior sites when compared with dark and light edges (Table 3). There was no significant difference between the first recordings at light and dark edges ($p > 0.05$). *Nyctophilus* spp. showed the same pattern (Table 3), again with no difference between first recordings at light and dark edges ($p > 0.05$). There was no difference between first recording times of *Vespadelus vulturnus* at both dark interior sites and dark edges (Table 3). However, first recording time was significantly later at light edges than at dark interior sites (Table 3) and dark edges ($p = 0.008$).

Overall, the first activity of the light-exploiting functional group was not significantly different across light treatments (Table 3), but there were species-specific responses. First activity of the light-exploiting *C. gouldii* was not significantly different across light treatments, however it was first
recorded significantly earlier in the night in connected forest than in patches (Table 3). Emergence time in connected forest averaged $151.9 \pm 9.1$ minutes after sunset, versus $203.1 \pm 16.9$ minutes after sunset in isolated forest patches. The time of first activity for *O. ridei* was significantly earlier at dark interior sites than at both light and dark edges (Table 3). *O. ridei* was also recorded significantly earlier at light edges than at dark edges ($p = 0.001$).

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

### 3.4 Insect responses

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

### 4. Discussion

Our study demonstrates the disruptive effects of artificial light at the edges of urban forest on light-sensitive and light-exploiting insectivorous bats. Our findings are consistent with research that artificial light has a negative effect on certain species in ecologically sensitive habitat (Straka et al. 2016) and that artificial light at the urban forest edge contributes to a loss of functional connectivity (LaPoint et al. 2015). Streetlights at the forest edge negatively affected the activity of the putative light-sensitive group of bats. Sydney’s smallest species, *V. vulturnus* was particularly negatively
affected by light, being less active and emerging later at artificially lit edges when compared with dark edges. Despite light edges having greater vegetation cover with 250 m, bat activity and richness was still lower here than at dark edges. Available functional habitat in urban forests is reduced by artificial light, and with some species unable to cross lit areas (Hale et al. 2015), urban biodiversity may continue to decline unless the degrading impacts of ALAN are addressed.

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

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

Recent multi-taxa research concluded that large connected patches of vegetation are critically important for urban biodiversity (Beninde et al. 2015). Our data supports this, showing that total bat activity, the activity of the light-sensitive species and *C. gouldii* were consistently higher on forest interiors when compared with edges. *Nyctophilus gouldi* were rarely recorded anywhere but bushland interiors, demonstrating the importance of forest interiors for bat diversity in cities.
With regards to insect trapping, Lepidoptera numbers were lowest at light edges, suggesting that the biomass was made up of fewer but larger individuals. We conclude that our findings are consistent with others (Pintérné and Pödör 2017), and may have been due to streetlights in the lit conditions outshining our light traps, and attracting most of Lepidoptera away from the trap. In future studies, suction traps (Shortall et al. 2009), sticky traps, malaise traps (Hosking 1979, Hallmann et al. 2017) or camera traps (Rydell 1992) may be better alternatives for sampling phototactic insects in artificially lit conditions.

4.1 Mechanisms driving light sensitivity in insectivorous bats

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

In comparison, 92 % of calls identified as *Nyctophilus* spp., the species group adapted to foraging in cluttered vegetation, were recorded at interior sites. Although *Nyctophilus* spp. have been observed using open and edge habitat in woodland (Brigham et al. 1997), our study confirms low activity of this species at the urban forest edge, regardless of whether streetlights were present or not.
Artificial light at the forest edge did not further reduce the low activity of *Nyctophilus* spp at these locations. Our findings are consistent with a previous study that found that movements of these taxa were mostly restricted within the bounds of an urban forest remnant (Threlfall et al. 2013). These taxa appear to be light-sensitive (Threlfall et al. 2013), but the lack of edge habitat use suggests both habitat fragmentation and disruption in the connectivity of dark vegetation across cities have critically impacted the urban survival of this group. Some bats, including *Nyctophilus* spp., could have retained a sensitivity to ultraviolet light (Gorresen et al. 2015), and this may cause these species to avoid streetlights emitting ultraviolet, like the ones in this study.

### 4.2 The importance of dark connected forest for urban bats

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

### 4.3 Artificial light altering the competition for resources

Niche differentiation between bat species can sometimes be subtle (Krüger et al. 2014) as bats exploit slightly different insect prey in similar habitat. Clutter-adapted bats will glean moths and beetles from the ground and from leaves, whereas open-space adapted bats will pursue prey on the wing (Denzinger and Schnitzler 2013). Artificial light sources are known to attract insect prey out of dark habitat and deplete foraging grounds for light-sensitive species (Rydell 1992, Rydell and Racey...
Our data supports this effect, where overall moth biomass was significantly higher at lit edges compared to dark edges and interior sites. Overall moth numbers did not follow the same pattern, suggesting that larger insects dominated near streetlights. This potential “vacuum cleaner effect”, where phototactic insects migrate out of dark forest and towards artificial light, may be decreasing the amount of available prey to bats restricted to dark areas, making it harder for them to persist in cities (Arlettaz et al. 2000). Investigation is needed into the extent of this depletion of dark foraging grounds for light-sensitive bats. Our data shows that light-sensitive bats are less likely to use artificially lit edges, and would therefore be less able to access the increased insect biomass there. Similar to previous experiments, artificial light sources could be creating foraging areas that mainly light-exploiting bats can exploit (Arlettaz et al. 2000, Stone et al. 2015). ALAN, particularly artificial light sources at forest edges in cities, may be disrupting the important environmental niches that allow bat species to co-exist.

4.4 Light as an edge effect

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

4.5 Lunar phobia and light phobia
Light phobia could be driven by an innate lunar phobia, with changing moon phase and the brightness of the moon linked to the emergence time and behaviour of some light-sensitive species such as *V. vulturnus* and others (Law 1997, Saldaña-Vázquez and Munguía-Rosas 2013). Lunar phobia is linked to morphological traits associated with foraging strategy; slow-flying bats respond more negatively to bright moonlight (Saldaña-Vázquez and Munguía-Rosas 2013). These species are also more likely to emerge later in the evening (Jones and Rydell 1994), theoretically because they are adapted to hunting prey available in the darkest part of the night and so avoid crepuscular predator peaks. Our data confirms this trend, that slow flying bat species avoid artificial light. This morphological group may be responding negatively to artificial light as they have evolved to respond negatively to moonlight. The species-specific differences here warrant further research.

Faster flying bats, those that appear more exploiting of artificial light, are less affected by moonlight (Saldaña-Vázquez and Munguía-Rosas 2013). These species may be pre-adapted, or at least resilient, to artificially lit environments. However much like the drivers of light phobia in bats, the mechanisms driving lunar phobia are difficult to pinpoint. Periods of bright moonlight are associated with reduced levels of insect prey (Lang et al. 2006), and may leave bats more vulnerable to predation (Law 1997), particularly important for slow flying bats. Very few studies have provided evidence that predation risk for bats increases under moonlit skies, even though it is discussed frequently in the literature (Saldaña-Vázquez and Munguía-Rosas 2013, Stone et al. 2015). Future studies teasing apart the causes of artificial light phobia, changes in food availability or predation risk, would elucidate the mechanisms influencing lunar and light phobia in bats.

**4.6 Future directions and conclusions**

In urbanized Sydney, five species are at particular risk of ALAN degrading viable habitat. Elsewhere the impact may be greater, for example; locations like tropical Barro Colorado Island in Panama are home to a much higher proportion of slower flying bat species (Denzinger et al. 2017). If the parameters of light sensitivity discussed here are applied to other bat communities, many more
species could be identified as at risk of habitat loss due to urban lighting at the edges of natural forest. This is an issue for particular consideration in expanding cities and peri-urban areas. Lighting near ecologically important areas, like drinking troughs, is already established as having a disruptive effect on bat drinking behaviours (Russo et al. 2017, Russo et al. 2018). Foraging by many bat species is affected also, and like others (Spoelstra et al. 2015, Straka et al. 2016), we recommend avoiding the installation of streetlights near ecologically sensitive areas in cities, such as native forests and wetlands. Other mitigation strategies, such as part night lighting, may be an alternative to constant lighting (Azam et al. 2015); but need to be turned off early enough in the night to successfully mitigate the impact on vulnerable species. If lighting near ecologically important forest is necessary, red lights (usually between 620 and 750 nm) have been shown to have minimal effect on a variety of mammal taxa (Spoelstra et al. 2015, Spoelstra et al. 2017), although their suitability as a bat-friendly alternative is controversial (Voigt et al. 2018) and needs further testing. LED technology allows lights to be manufactured to emit specific spectra, which has recently been found to be useful for minimising disruption for bats (Haddock et al., in press). Research could be used to help manufacturers create lights with the least disruptive spectra for nocturnal biodiversity. However, conserving dark forested areas in cities remains crucial for the persistence of nocturnal biodiversity such as light-sensitive insectivorous bats.

5. Role of the funding source

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6. Acknowledgements

I would like to thank Kyle Armstrong at Specialized Zoology for the loan of the Anabat II detectors. This research was supported by the Australian Government’s National Environmental Science Program through the Clean Air and Urban Landscapes Hub.
References


http://ro.uow.edu.au/theses/3702


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

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

<table>
<thead>
<tr>
<th>Category</th>
<th>Measurement</th>
<th>Response variable</th>
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<td>BAT ACTIVITY</td>
<td>Average activity;</td>
<td>all bats</td>
</tr>
<tr>
<td></td>
<td></td>
<td>the light-exploiting group</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Chalinolobus gouldii</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Ozimops ridei</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td>the light-sensitive group</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Nyctophilus spp.</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Vespadelus vulturnus</em></td>
</tr>
<tr>
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</tr>
<tr>
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<td></td>
<td>for light-exploiting group</td>
</tr>
<tr>
<td></td>
<td></td>
<td>for light-sensitive group</td>
</tr>
<tr>
<td>BAT EMERGENCE TIMES</td>
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<td>for the light-exploiting group</td>
</tr>
<tr>
<td></td>
<td></td>
<td>for the light-sensitive group</td>
</tr>
</tbody>
</table>
**Chalinolobus gouldii**

**Ozimops ridei**

**Nyctophilus spp.**

**Vespadelus vulturnus**

**INSECT ABUNDANCE**

- Averages: number of Lepidoptera collected
- Biomass of Lepidoptera

---

a) Total bat activity

b) Light sensitive bat activity

c) Light tolerant bat activity

d) *Chalinolobus gouldii* activity

e) *Ozimops ridei* activity

f) *Vespadelus vulturnus* activity
Figure 3. Plots showing marginal means ($\pm 1$ s.e.) after controlling for site. Figure 3a. Bat activity compared across light treatments; Figure 3b. Activity of the light-sensitive group compared across light treatments; Figure 3c. Activity of the light-exploiting group compared across light treatments; Figure 3d. Activity of *C. gouldii* compared across light treatments; Figure 3e. Activity of *O. ridei* compared across light treatments; Figure 3f. Activity of *V. vulturnus* compared across light treatments; Figure 3g. Species richness of the light-sensitive group compared across light treatments; Figure 3h. Lepidopteran biomass (mg) compared across light treatments. Statistically significant differences when comparing variable measurements between treatments are depicted using differing letters (a, b and c).
Table 2. Results of GLMM with habitat type and light treatment as fixed effects, and site as a random effect, with response variables listed on the far left column, and the dark interior control treatment and patch treatment as the reference categories

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>p value</th>
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<td>Average light-exploiting species activity</td>
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<td>0.1863</td>
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Figure 4. Average percentage (± se) of light-sensitive and light-exploiting functional group echolocation calls recorded at light edge sites and at dark edge sites. Calculated by combining calls for each site with calls from associated interior control site and then calculating the percentage of the total calls recorded at the edge.

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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard error</th>
<th>t value</th>
<th>p value</th>
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</thead>
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<tr>
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<tr>
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<td>Connected forest versus patch</td>
<td>-53.183</td>
<td>20.6049</td>
<td>-2.581</td>
<td>0.013</td>
</tr>
<tr>
<td>Light edge versus interior</td>
<td>-15.014</td>
<td>23.1303</td>
<td>-0.649</td>
<td>0.519</td>
</tr>
<tr>
<td>Dark edge versus interior</td>
<td>26.846</td>
<td>24.3959</td>
<td>1.100</td>
<td>0.276</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Minutes until first <em>O. ridei</em> activity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>5.272</td>
<td>0.1409</td>
<td>37.419</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Connected forest versus patch</td>
<td>-0.129</td>
<td>0.1919</td>
<td>-0.672</td>
<td>0.506</td>
</tr>
<tr>
<td>Light edge versus interior</td>
<td>0.176</td>
<td>0.0333</td>
<td>5.291</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Dark edge versus interior</td>
<td>0.376</td>
<td>0.0419</td>
<td>8.961</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Figure 5. Activity of light-sensitive bats throughout the night. This is calculated by noting sunset and sunrise each night of the survey and calculating what percentage of the night had elapsed when each call was recorded. The graph shows the number of calls recorded within each 10 percent increment throughout the night. The bottom graph shows the combined data from the edge sites compared with the data from the interior sites.

Appendix

Insect sampling

Insects were sampled at the edge and interior locations of all patch sites (n = 30) for one night. For each patch, the edge and the interior were sampled on the same night to control for variation across nights. Sampling took place two weeks after acoustic sampling to avoid interfering with naturally occurring bat activity, however temperature and humidity were not significantly different and so insect sampling nights were deemed comparable to bat sampling nights. We avoided surveying on full moon and new moon nights, and for 3 days either side of both events. Black light intercept traps (Australian Entomological Supplies, Murwillumbah, Australia) were placed on the ground, in the same location used for the Anabat II detectors two weeks prior, less than 3 m from the base of the streetlight pole. 50ml of ethyl acetate was added to the bottom of the light trap, bulbs were attached to 12V batteries, and the trap was turned on between 2000 and 2300. Excalibur digital timers (Merlin Distribution, Roseville, Australia) automatically turned the lights off after 2
hours, and traps were collected within an hour of the light turning off. Individual insects were then
separated and identified to order. Only Lepidoptera were included in the analysis as only a small
number of insects of other orders, Dipterans and Coleopterans, were caught. Body length of each
individual insects was measured, and biomass was calculated using established methods (Sample et
al. 1993).

ii Limitations of insect surveys

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

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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard error</th>
<th>t value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass of Lepidoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>5.731</td>
<td>0.0955</td>
<td>60.003</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
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<td>--------------------------------</td>
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<td>--------</td>
<td>--------</td>
<td>--------</td>
</tr>
<tr>
<td>Connected forest versus patch</td>
<td>0.143</td>
<td>0.3798</td>
<td>0.375</td>
<td>0.710</td>
</tr>
<tr>
<td>Light edge versus interior</td>
<td>0.244</td>
<td>0.0309</td>
<td>7.896</td>
<td>0.000</td>
</tr>
<tr>
<td>Dark edge versus interior</td>
<td>-0.104</td>
<td>0.0262</td>
<td>-3.979</td>
<td>0.000</td>
</tr>
</tbody>
</table>

Average number of Lepidoptera caught

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>3.209</td>
<td>0.1598</td>
<td>20.080</td>
<td>0.000</td>
</tr>
<tr>
<td>Connected forest versus patch</td>
<td>-0.533</td>
<td>0.6323</td>
<td>-0.843</td>
<td>0.407</td>
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<tr>
<td>Light edge versus interior</td>
<td>-0.546</td>
<td>0.1289</td>
<td>-4.239</td>
<td>0.000</td>
</tr>
<tr>
<td>Dark edge versus interior</td>
<td>0.126</td>
<td>0.0845</td>
<td>1.495</td>
<td>0.146</td>
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</table>