RESEARCH ARTICLE

ethology *International journal of behavioural biology* WILEY

Insects within bushes assemble and forage closer to artificial light at night

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Editor: Tom Tregenza

Abstract

Artificial light at night (ALAN) has been implicated in the global decline of insect populations. Causal mechanisms contributing to declines remain unclear, however. Here we examine causal factors which could link some declining terrestrial insect populations with ALAN. To do so, we defined the closest and furthest halves of individual bushes according to the nearest source of artificial light. We sampled leaves and invertebrates from both sides to determine herbivory and abundance. First, we observed that, within bushes, leaves were significantly more likely to display herbivory at closer distances to established streetlighting. This may be due to the phenomenon of positive phototaxis in insects (flight to light). Further, insects within bushes were significantly more abundant on the side closest to streetlighting at midnight, but not at midday, when lights are unilluminated. Consequently, we argue that ALAN creates bottom-up trophic effects, driven by insect light attraction behaviours even at the scale of single plants.

KEYWORDS
abundance, ALAN, herbivory, positive phototaxis, terrestrial insects, trophic effects

1 | INTRODUCTION

Artificial light at night (ALAN) such as streetlighting is likely a key factor in global insect declines (Owens & Lewis, 2018; Owens et al., 2020; Wagner, 2020; Wagner et al., 2021). In the UK alone, between 30% and 60% of insect species are estimated to be in decline (Dirzo et al., 2014), which might be linked to nearly half of Europe experiencing greatly modified day-night light cycles (Falchi et al., 2016). Causation, however, is tenuously established. It has been suggested, for example, that the intrusion of light into otherwise dark night-time environments disrupts insects' foraging behaviour (Cieraad et al., 2022; Tierney et al., 2017; van Langevelde et al., 2018) and decreases the nutritional bioavailability of their hostplants (Grenis & Murphy, 2019); but whether this ultimately affects herbivorous insect abundance is unclear. Some researchers have reported that, at broad scales, insects are less abundant near streetlighting (Boyes et al., 2021b), whilst others report abundance levels which are the same, species-dependent, or greater near various forms of ALAN (Firebaugh & Haynes, 2020; Hakbong et al., 2021; Lockett et al., 2021; Manfrin et al., 2017; McMunn et al., 2019; Willmott et al., 2019).

Clearly, there is still much to be unravelled in the relationship between ALAN and insect declines, with several recent reviews calling for carefully designed experimentation and study investigating the relative importance of various causal factors (e.g. Boyes et al., 2021a; Wagner, 2020). Here we seek to contribute to this by exploring whether ALAN has effects on the distribution and herbivorous behaviour of insects at small spatial scales within individual bushes.

Previous studies have generally found that herbivory by insects was greater under higher levels of light (Cieraad et al., 2022; Mondy et al., 2021; Schroer et al., 2019). Thus, it was hypothesised that herbivory might be greater under higher luminance even within individual plants. If this were true, we predicted that invertebrate abundance within a bush would not differ greatly across the distance from the light source by day, but that greater numbers of insects would be found on the side of bushes closest to the nearest source of artificial light by night. As a light source, we used urban streetlights, since these are very widespread geographically and since they are well-established year-round sources of ALAN. We carried our study out in St Andrews in Scotland, in localities where the buildings are over a century old, and so the locations of lampposts for streetlighting will have been well-established in comparison to the lifetimes of local flora and fauna.

2 | MATERIALS AND METHODS

2.1 | Within-plant herbivory distribution

Existing LED streetlight lampposts around St Andrews (UK) were used to investigate the effect of varying levels of ALAN on invertebrate herbivory of nearby shrubs. Sites were selected where a bush (defined for these purposes as a shrub or clump of shrubs of a single species forming a bush of determinate size) could be found with its closest side no more than 6 m from the nearest lamppost; see Figure 1. We have previously found using a luxmeter, that illumination at ground level falls from an average of 14.3 lux ($\sigma = .6$) directly below the filament, close to ambient 6 m away from these streetlights (Eckhartt & Ruxton, 2022). Selected bushes were also of maximum 6 m diameter at the widest point and could be divided into clearly defined halves, being either the "closest" or "furthest" sides of the bush, separated by a line drawn perpendicular to a vector connecting the centre of the bush with the nearest lamppost (Figure 1). Bushes were selected only where a direct line of sight between the nearest lamppost filament and the closest side of the bush could be established, and only where at least 90% of their outward-facing surface area was accessible to an experimenter. In addition, bushes were selected where the leaves of that species are generally large and un-needled, such leaves being more conducive to analysis using leaf surface-area approximation software (see later). At each bush, the distance from the lamppost to the closest and furthest edge of the bush was measured. A map of sample sites can be found in Figure S1.

Ten leaves were collected from each of the furthest and closest sides of 28 focal bushes on July 1, 2022. The leaf collector was blind to the experimental procedure and hypotheses under test. They were directed, by the non-blind experimenter (G.M.E), only as to the dividing line which delineated the two halves of each bush, and were requested to pick 10 leaves at random from each side, with no preference as to leaf size, completeness, quality or location (see examples in Figure 1). The underside of each leaf was marked by the non-blind experimenter using a Sharpie, denoting which side of the bush the leaf had been taken from. They were then placed in plastic bags marked with bush ID for later analysis.

Leaves were analysed using LeafByte (Getman-Pickering et al., 2020), an iOS application which calculates the surface area of a leaf using image analysis with given pixel intensity thresholds and a scale of known size. A photograph was taken of each leaf using an iPad mini 4 on a white background, with a scale of four black dots separated by 17 cm each. Each leaf was flattened by a clear plastic screen to minimise shadows created by the leaf and best approximate the two-dimensional surface. The software receives the image and determines the surface area of the leaf by counting the number of pixels which exceed an intensity threshold determined by the experimenter using a sliding scale. Any pixels enclosed within the leaf which do not exceed the threshold, i.e., where there is a hole created by leaf tissue removal, are counted as consumed leaf area. Where herbivory had occurred on the edges of a leaf, a line had to be drawn by the experimenter, approximating where the leaf outline would have been, before this was counted by the software as consumed leaf area. There were two potential areas of experimenter subjectivity inherent in this process; that of the pixel intensity threshold and that of the lines drawn by the experimenter. In order to eliminate bias, leaves were analysed face-up, without revealing the underside which coded the side of the bush from which the leaf was taken, until after the leaf had been fully analysed.

2.2 | Within-plant invertebrate distribution

To estimate the effect of ALAN on insect abundance within bushes, 11 bushes from the herbivory experiment described above were beaten with a wooden club on July 27 and again on August 9 (2022, St Andrews). This method is well established for estimating within-plant invertebrate abundance, and often referred to as "hedgerow-beating" (e.g. Boyes et al., 2021b; Gardiner, 2010). Once the closest and furthest sides of the bush had been delineated in accordance with the methodology described in section 2.1, a 72×80 cm pale cotton sheet was placed directly below the bush on each side; see Figure 1. Identical sheets were placed under the "near" and "far" sides of the bush, meeting at their dividing line. The focal bush was beaten with a wooden club and invertebrates of any kind which had fallen from the bush onto the two sheets were then counted and recorded simultaneously by two experimenters. One experimenter was blind to the procedure and hypotheses, whilst the other (G.M.E) was not. To minimise any effects of bias, the side (near or far) counted by each experimenter was swapped for each new bush and count differences by experimenter were later analysed. On the first day, five bushes were beaten at midday (circa 12:00 p.m.) when lampposts are off. Six different bushes were then beaten at the following midnight (circa 12:00 a.m.) when lampposts are illuminated. On the subsequent day of beating, those bushes which had been beaten at midday were beaten at midnight and vice-versa, providing an even number of counts across times of day and locations. It was
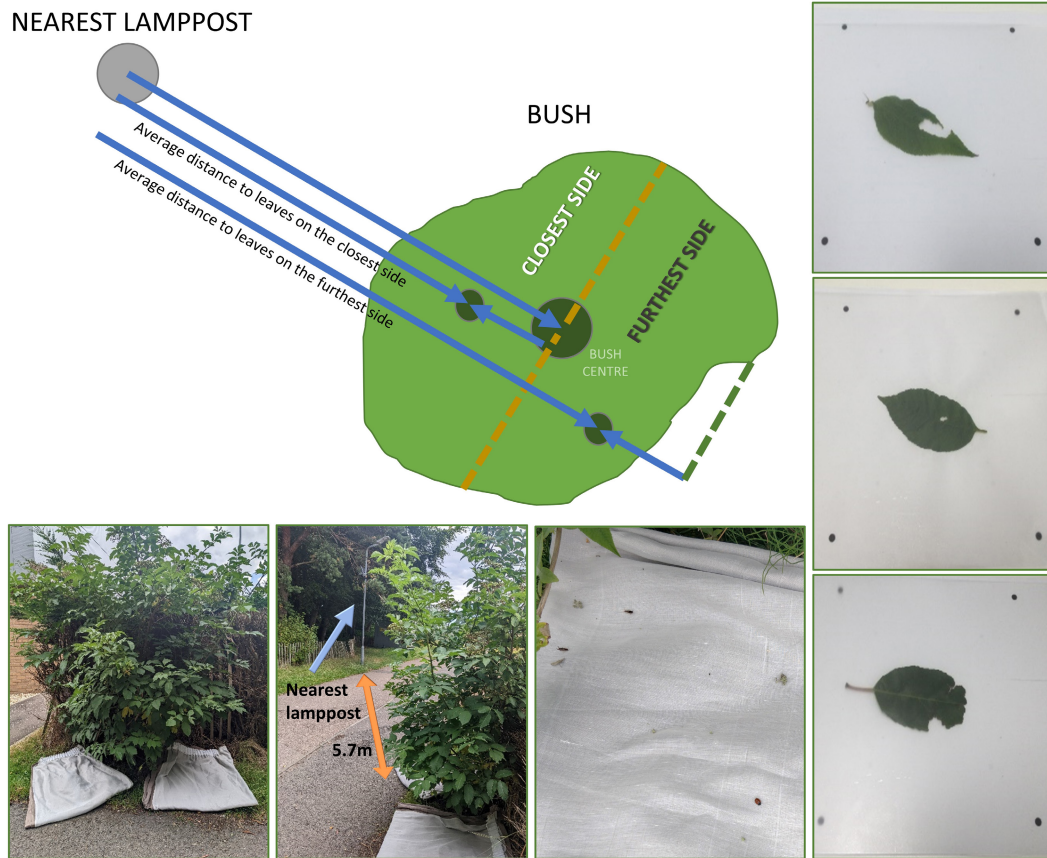
FIGURE 1 Top left: Bush delineation. Two halves of each focal bush were designated on either side of a bisecting line drawn perpendicular to a vector connecting the centre of the bush with the nearest lamppost. The average distance of leaves taken from either side was estimated as halfway between the centre of the bush and the furthest or closest edge of the bush in relation to the lamppost. Bottom left 3 images: Hedgerow-beating setup is depicted, with sheets placed under two halves of a focal bush, being the closest and furthest halves from the nearest lamppost. The centre of this bush was approximately 5.7 m distance from the lamppost. The right-most image shows a slice of the sheet in the aftermath of beating, with several insects having fallen from the bush onto the sheet. Right 3 images: Three leaves displaying signs of herbivory, taken from specified sides of various bushes in St Andrews. The top and bottom-most leaves required estimation of the edges prior to herbivory in leaf analysis.

assumed that 13 days between each round would suffice to minimise any effects of prior disturbance. The animals sampled in this study were STRANGE by virtue of their limited geographic dispersal and, in some cases, likely propensity for positive phototaxis (Webster & Rutz, 2020).

2.3 | Statistical analysis

Data were analysed in R v 4.0.4 (R Core Team, 2021). For the herbivory study, data distribution was analysed using histograms and basic plots. This revealed that the response variable was highly zero-inflated and over-dispersed, with some leaves having displayed no herbivory and others having a very large relative surface area consumed. The response variable was converted to binary, assigning a '1' where the surface area consumed was non-zero, and a '0' where there was no apparent surface area consumed, thus effectively modelling the chance that a random leaf displays any

signs of herbivory. The main effects of the model were then assessed using a binomial (logit) generalised linear mixed model (GLMM) with the package lme4 (Bates et al., 2014). The sole explanatory variable in the model was the distance from the lamppost (taken as the distance from the lamppost to the halfway point between the bush centre and either the closest or furthest edge of the bush from the lamppost; see Figure 1); its effect on the chance of herbivory being assessed within bushes by the inclusion of bush ID as a random factor. AIC and AUC confirmed that the logit link best fit the data (Akaike, 1998; Bamber, 1975; Matthiopoulos, 2011). We also assessed whether leaf surface area (including the estimated damaged area) differed within bushes by distance, using a linear mixed effects model (LMM). Degrees of freedom and p-values were estimated for this test using the lmerTest package (Kuznetsova et al., 2017).

For herbivore distributions, the main effects were analysed using a Poisson (log) GLMM with the package lme4 (Bates et al., 2014). The response variable was invertebrate count, with the final model

including categorical time of day (concomitant with lights on/ off) and categorical side of the bush (close or far from nearest lamppost, associated with varying lux levels at night), as explanatory variables. These effects were assessed within bushes by the inclusion of day nested within bush ID as random factors. Unlike the herbivory analysis, for the analysis of abundance data, we were not able to code distance accurately as we could not control the distance at which samples were taken as insects may not be distributed evenly across each side of the bush. We could only control which side of the bush they were sampled from. Thus, the side of the bush was encoded as a discrete factor in the model (as opposed to continuous distance from lamppost). AIC and percentage deviance confirmed that the log link best fit the data (Akaike, 1998; Bamber, 1975; Matthiopoulos, 2011). Post-hoc pairwise Tukey's tests (Tukey, 1977) were performed on the marginal mean responses at each side of the bush at each time period, estimated using the emmeans package (Lenth, 2022).

3 | RESULTS

3.1 | Herbivory

Of 556 leaves analysed (4 were damaged in transit), 258 (46%) displayed signs of herbivory.

When modelling within-bushes, we found no evidence that leaves differed significantly in overall surface area (LMM, effect of distance in model investigating leaf area $t_{133} = -.25$, $p = .803$). However, we found that leaf herbivory was significantly less likely as distance increased (GLMM, effect of distance in full model $z_{553} = -1.997$, $p = .046$; Figure 2; full table and illustrative means and standard deviations are given in Tables S1–S4).

3.2 | Invertebrates

In total, 183 insects were counted at midday and 352 at midnight.

When modelling within-bushes, invertebrate count was significantly lower on the side of the bush furthest from lampposts (GLMM, effect of side in full model $z_{19} = -4.149$, $p < .001$; full table and illustrative means and standard deviations are given in Tables S1–S4). This effect interacted significantly with time of day (GLMM, interaction effect of side and time: $z_{19} = 2.291$, $p = .022$). Post hoc analyses revealed that the estimated marginal mean count was significantly higher on the close side of bushes at midnight (pairwise Tukey's test, $z = 4.149$, $p < .001$; Figure 3), but not at midday (pairwise Tukey's test, $z = .224$, $p = .996$).

A model with simply day nested within bush ID as random factors and experimenter ID included as the sole explanatory variable, revealed that counts on average did not differ significantly between experimenters (GLMM, effect of experimenter, $z_{40} = -.305$, $p = .760$).

4 | DISCUSSION

The ways in which night-time lighting might contribute to insect declines are likely numerous and interacting. Our results indicate that ALAN may alter insect foraging behaviour even at very small spatial scales, which in turn may be a factor in such declines. Previous studies have found that greater levels of light generally enhance herbivory (Barber & Marquis, 2011; Mondy et al., 2021; Schroer et al., 2019). This is largely thought to be the result of positive phototaxis exhibited by herbivorous insects, such as some moth larvae (Buck & Callaghan, 1999; De Ruiter & Van Der Horn, 1957; Donners et al., 2018; Eccard et al., 2018; McMunn et al., 2019); although there
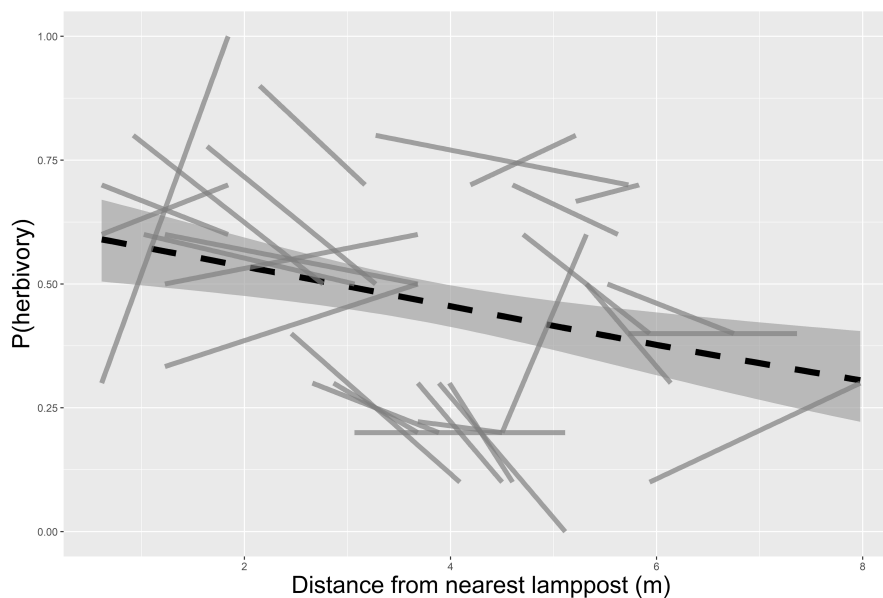

FIGURE 2 The final model predicts that, within bushes, chance of herbivory decreases significantly with increasing distance. Solid grey lines represent a glm fit of the observed data for each bush. The dashed black line represents an overall glm fit of the final model prediction, with a 95% confidence ribbon.
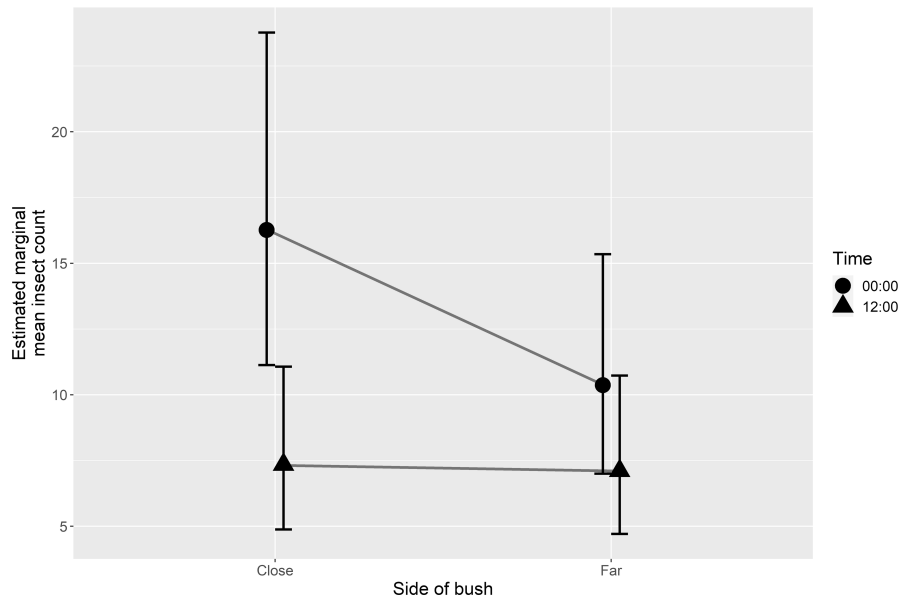
FIGURE 3 Plot of estimated marginal mean insect count within bushes, across the furthest and closest halves of the bush from the nearest source of artificial light, at midnight and midday, according to the final generalised linear mixed model. Insect count is estimated to reduce significantly across sides of the bush for midnight only, with no significant change estimated at midday. Error bars represent 95% confidence.

exists insufficient evidence across a wide enough range of taxa to evaluate the generality of this. Consistent with this hypothesis, we found a possible enhancing effect of ALAN on herbivory on the small spatial scale of within an individual bush.

Positive phototaxis is potentially detrimental to invertebrate herbivore fitness, in at least some circumstances, as it may override the tendency to forage on patches of higher quality resources. Indeed, whilst plant biology can be highly altered under ALAN (being intrinsically connected to light levels (Bennie et al., 2016; Vänninen et al., 2010)), generally to the detriment of herbivores, insects are still found to preferentially forage under ALAN. Evidence suggests that ALAN can suppress flowering (Bennie et al., 2015, 2018) and reduces plant quality via increases in the carbon-to-nitrogen ratio and plant toughness, limiting nutritional value and bioavailability (Grenis & Murphy, 2019; Murphy et al., 2022). It follows then, that a tendency to forage closer to artificial light sources could be deleterious to herbivorous invertebrate foraging efficiency. Indeed, consumption by insects of plant matter grown under ALAN, versus plant matter which was not, has been shown to result in lower eventual mass (Grenis & Murphy, 2019; Péter et al., 2020). Ultimately, this might reduce survival and lower fitness. However, effects of ALAN on plants are complex and can include advancing budburst and delaying leaf senescence in the autumn, which in theory should provide more high-quality food for herbivores (Ffrench-Constant et al., 2016; Schroer et al., 2019). In the end though, whilst evidence suggests that ALAN may alter leaf quality between-plants, whether leaf quality differs within-plants is not well-established. We found no evidence that leaf size was affected by distance from nearby lampposts within-bushes. Further study is thus recommended which investigates the effect of ALAN on leaf quality, such as carbon-nitrogen

ratio, within individual plants. Another useful development of the results reported here would be to explore to what extent the increased herbivory seen on the side of bushes nearest the streetlights was due to increased herbivore numbers, change in herbivore diversity and/or increased activity by herbivores.

Insect abundance has previously been estimated across lit and unlit sites within an ecosystem. More often than not, insects were more abundant at lit sites (Davies et al., 2012, 2017; Lockett et al., 2021); although there is some contrasting evidence (Boyes et al., 2021b; Lockett et al., 2022). We have shown that ALAN is linked to increases in insect abundance even at very fine temporal and spatial scales, displaying an effect of artificial light at night within individual plants that changed from daylight distributions just hours before. We found that insects were significantly more numerous at midnight in the half of bushes which was closest to the nearest lamppost, but found no effect of bush side at midday. Whilst other factors such as proximity to roads might also correlate with the side of bushes closest to streetlighting, the effects of such factors on abundance would not necessarily be expected to differ by day and night; or if so, they might be expected to affect abundance at busier times of day (i.e. closer to midday, when we found no effect of side). Thus, we believe that the present results present a strong argument for a direct effect of ALAN on insect abundance within bushes, which might be explained by positive phototaxis (Buck & Callaghan, 1999; De Ruiter & Van Der Horn, 1957; Donners et al., 2018; Eccard et al., 2018; McMunn et al., 2019). Future experiments could seek to confirm this through direct experimental manipulation of insects sampled from either side of focal bushes, perhaps through the use of a Y-maze with lit and unlit branches. Alternatively, positive phototaxis may have caused insects to aggregate on the

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closest side of nearby bushes, which effect persists into the day but was then counteracted by daytime effects such as busier roads. We do not deem this to be likely, as evidence to date generally suggests that there are enhancing or no road-proximity effects, such as via nitrogen content and de-icing salt, on insect abundance within plants (Muñoz et al., 2015).

The effects we found will inherently vary with, be influenced by and affect other trophic processes. For example, insectivorous spiders have also been found to forage preferentially closer to ALAN (Willmott et al., 2019), perhaps because of greater prey abundance and capture rate, but also causing greater mortality of herbivorous insects closer to light. This effect might be especially enhanced in the context of visual predators, which enjoy a greater insectivory success rate under light than not at night (Miller et al., 2017; Taylor et al., 2022). Conversely though, insectivores sitting at an intermediate trophic level are probably inclined to forage further away from ALAN (Aparício et al., 2022; Eckhartt & Ruxton, 2022), which could reduce mortality closer to light and conceivably might cause greater abundance. However, evidence also suggests that there may be circumstances under which food preference (i.e. sites of higher abundance) overrides this tendency in such animals (Aparício et al., 2022). Indeed, the ecological effects of ALAN are not always simple. Only with continued experimentation and study, considering and excluding various interactions and effects, might we untangle the underlying mechanisms. One limitation of our study was that we did not identify insects even to functional group level. A useful future development building on our work would be to explore the relative contributions of different groups to the effects reported here. Particularly interesting would be comparing herbivorous insects and their potential predators.

5 | CONCLUSION AND SIGNIFICANCE

We found that, within bushes, insects were more abundant on the side closest to sources of artificial light at midnight, but not at midday. Furthermore, we found that leaves taken from the same side of such bushes were more likely to display herbivory than those further from ALAN. This may detriment insect fitness via bottom-up trophic effects associated with the lower nutritional quality of leaves and plants grown under ALAN. More than 23% of Earth's terrestrial environments between 75°N and 60°S are estimated to be polluted by light at night, providing a worrying impression of the global potential for ecological disturbance by ALAN (Falchi et al., 2016). Trends suggest that this is likely to continue to increase (Kyba et al., 2017, 2023). Action is urgently required to mitigate the negative impacts of ALAN. Although the benefits of ALAN for human well-being are clear, some strategies such as shielding, timers or motion-activation, which compromise little in terms of human benefits, could go some way toward this goal at minimal cost (Gaston et al., 2012). Our experiments build upon a growing base of evidence linking ALAN with the decline of terrestrial insect populations. It is hoped that the present research provides a valuable contribution in understanding the

role of ALAN in such declines. In turn, we hope that such research can contribute to urban planning and the implementation of artificial lighting given the continuing urbanisation of our planet.

AUTHOR CONTRIBUTIONS
Gregory M. Eckhartt: Conceptualization; methodology; data curation; formal analysis; writing – original draft; investigation. **Graeme D. Ruxton:** Conceptualization; writing – review and editing; supervision; methodology.

ACKNOWLEDGMENTS
L. Garbutt, M. Gévaudan & A. Vegh are thanked for assisting with data collection. A. Vegh is also thanked for discussing methodology. The University of St Andrews is acknowledged for providing the resources and support necessary for the completion of this research. We thank three reviewers for their very valuable comments and suggestions.

FUNDING INFORMATION
This work was supported by the University of St Andrews.

CONFLICT OF INTEREST STATEMENT
The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT
The datasets generated during and/or analysed during the current study are available in the OSF repository, https://osf.io/6s5tb.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Eckhartt, G. M., & Ruxton, G. D. (2023). Insects within bushes assemble and forage closer to artificial light at night. *Ethology*, *00*, 1–8. https://doi.org/10.1111/eth.13373