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Artificial light at night drives diel activity patterns of synanthropic pipistrelle bats and their prey

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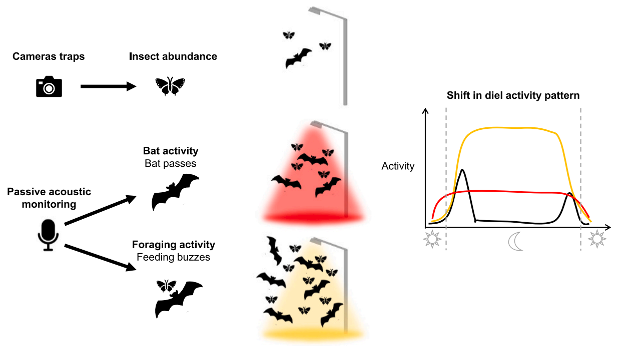
HIGHLIGHTS

- While most bats are light averse, some exploit insects' aggregation around light.
- Insects and bats are more active throughout the night due to artificial light.
- Artificial light facilitates all-night foraging in bats especially near white light.
- Natural activity patterns are less impaired by red light than white light.
- These results open the possibility of using spectral composition as a mitigation measure.

GRAPHICAL ABSTRACT



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ABSTRACT

The use of artificial light at night (ALAN) has increased drastically worldwide over the last decades. ALAN can have major effects on nocturnal communities, including insects and bats. Insects are attracted to street lights and few bat species take advantage of this by foraging on the attracted insects. ALAN potentially affects the temporal patterns of insect abundance and thereby bat foraging behaviour. In a natural dark environment, these patterns are usually bimodal, with an activity peak in the early evening and the morning. Little is known about how ALAN affects insect presence throughout the night, and whether the light spectrum plays a role. This is important, as these temporal changes may be a key driver of disturbances in bat-insect interactions. Here, we studied how white and red light affect insects' and bats' nightly activity patterns. The activity of insects and bats (*Pipistrellus* spp.) was recorded throughout the night at seven experimentally illuminated sites in a forest-edge ecosystem. ALAN disrupted activity patterns, with both insects and bats being more active throughout the night. ALAN facilitated all-night foraging in bats especially near white light, but these effects were attenuated near red light. The ability to forage throughout the night may be a key advantage causing synanthropic bats to dominate in illuminated environments, but this could also prove detrimental in the long term. As red light reduced disturbing effects of ALAN on insects and bats diel activity pattern, it opens the possibility of using spectral composition as a mitigation measure.

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1. Introduction

The use of artificial light at night (ALAN) has shown a drastic increase over the past decades (Falchi et al., 2016; Falchi and Bará, 2023; Kyba et al., 2017, 2023), mainly accelerated by the introduction of light-emitting diode (LED) lamps in outdoor lighting. ALAN disrupts natural light cycles in time and space and effects are wavelength-dependent (Gaston et al., 2013). Therefore, natural patterns of resource use by organisms exposed to ALAN may be altered, affecting a wide range of taxa, especially nocturnal animals (Sanders et al., 2021), including bats and insects.

Nocturnal insects are attracted by ALAN, especially by the UV and the blue component of the light spectrum (Donners et al., 2018). This can have negative impacts on their foraging (van Langevelde et al., 2017), reproduction (Owens and Lewis, 2022) and cause exhaustion or death (Eisenbeis, 2006), which can lead to population decline (van Grunsven et al., 2020). The attraction of insects from unlit to lit areas, also called the 'vacuum effect', subsequently alters the foraging opportunities of their predators such as insectivorous bats (Russo et al., 2019; Rydell, 1992).

Bats need to exploit spatial heterogeneity in food availability, and light sources offer predictable foraging locations with higher insect densities. While most bat species are light averse, a few others take advantage of insects' aggregation around light sources. Several *Pipistrellus* species are typical examples of synanthropic bats, as they commonly forage around street lights, where aerial insects aggregate (Bolliger et al., 2020b; Russo et al., 2019; Rydell, 1992; Spoelstra et al., 2017). However, bats' response is context-dependent, as Hooker et al. (2022) showed that the feeding activity of pipistrelles can decrease under lit treatments along waterways.

Under natural, dark conditions, flying insects often show a temporal pattern with a large activity peak around dusk and a smaller peak around dawn (Racey and Swift, 1985; Rydell et al., 1996; Swift, 1980). This is especially the case for dipterans, on which synanthropic bats like pipistrelles mainly prey upon (Rydell et al., 1996; Swift et al., 1985). Bats generally show the same bimodal pattern (Ciechanowski et al., 2009; Kunz, 1973; Mariton et al., 2023; Rachwald, 1992), so that their activity pattern is closely related to the temporal activity pattern of their prey (Erkert, 1982; Racey and Swift, 1985; Rydell et al., 1996; Swift, 1980). The lack of foraging activity in the middle of the night coincides with the lowest insect abundance (Racey and Swift, 1985). Bats may stop foraging with lower insect activity, and lactating bats can feed their young while waiting for the morning insect peak (Racey and Swift, 1985; Swift, 1980). The activity patterns of flying insects and bats have mainly been studied under natural conditions (Hayes, 1997; Mariton et al., 2023; Ruczyński et al., 2020; Russo et al., 2011; Rydell et al., 1996; Speakman et al., 2000; Swift, 1980), and little is known about the changes in their temporal patterns in response to ALAN (Azam et al., 2015; Hooker et al., 2022; Mariton et al., 2022). If insects shift their activity within the night, bats likely adjust their temporal activity to this.

To answer this question, a simultaneous and continuous assessment of bat and insect activity throughout the night is essential. Bats can effectively be monitored by recording bats' echolocation calls, but the measurement of insect activity is a challenge because most methods use light, which obviously will interfere with the light treatments (Froidevaux et al., 2018). Suction traps or flight-interception traps can be programmed for interval collection of insects (Bolliger et al., 2020a; Johnson, 1950), but this is logistically challenging, and collected insects are no longer available for bats. A solution is the use of infra-red (IR) cameras as these can capture insects in low light levels conditions (Rowse et al., 2018), but it enables a less specific census (Ruczyński et al., 2020).

In order to assess the impact of artificial light on the temporal activity pattern of light-tolerant bats and their prey, we simultaneously assessed nocturnal insect abundance, as well as foraging and feeding activity of synanthropic pipistrelles in response to different light spectra using camera traps and passive acoustic monitoring near experimental light posts in forest edge habitat. The activity of both aerial insects and bats was continuously recorded throughout the night to measure changes in their activity pattern in response to ALAN. We hypothesized that natural activity patterns are disrupted by artificial light. We predicted that the insect activity would be constantly high throughout the night in lit conditions, compared to a bimodal activity pattern in dark natural conditions. We predicted that these temporal changes in insect activity would drive alterations in foraging activity of bats.

2. Material and methods

2.1. Field sites and data collection

Insect abundance and bat activity were assessed in forest edge habitat at seven experimental sites in the Netherlands set up to study the effect of ALAN on the forest edge ecosystem. The forest edges border mostly heathland; the sites and the area around these are located inside nature reserves. Sites are described in more detail in Spoelstra et al. (2015). At each site insect abundance and bat activity were estimated under three different light treatments: white light (Philips Fortimo White), red light (Philips Fortimo Clearfield) as well as a dark control (wooden poles), around a 4 m tall lamppost placed at the forest edge. The distance between light treatments varied between 88 and 386 m (average 204 m; standard error, s.e. 17). All lampposts are programmed to be on from sunset to sunrise since spring 2012. The illuminance at ground level is 7.6 ± 1.2 Lux (1 s.e.m.) beneath each lamppost. Sensors connected to data loggers (BL30 Climate-Data Logger, Trotec, Germany) were programmed to record air temperature and relative humidity every 20 s to monitor weather conditions. The sensors were attached to the tripod on which we installed the microphones, at about 1 to 1.5 m above the ground. The study was carried out during 27 nights without rainfall and a minimum temperature (during the night) of 8 °C, between May 8th 2020 and August 9th 2020. Bat and insect activity were measured simultaneously at the three light treatments at one site per night. Data were included for analysis only if the bat recordings and the corresponding insect data from camera traps were complete for a full night. This resulted in 19, 19 and 18 nights of data for the control, red and white treatments respectively, with two to four nights per site (SI, Table S1).

2.2. Insect activity using camera traps

Insect abundance was continuously measured throughout the night with infrared interval photography, using Reconyx HC500 HyperFire Semi-Covert IR camera traps. Two camera traps were placed at 30 cm below the luminaire of each lamppost, one facing the direction of the light post (front) and the second one the opposite direction (back) (Fig. 1a), in order to detect insects at both sides of the lamppost. There was no vegetation in the close vicinity of the lamppost. Therefore, the camera traps' field of view was not obstructed and the insect detection was not impaired by vegetation. Cameras were set to take pictures every minute between 20:00 and 08:00 the next morning. Insects can be seen as white dots or short lines on the dark background (Fig. 1b), so species identification was not possible. Insects were counted manually using MapView Professional software (Reconyx, 2016).

2.3. Validating camera trap data using sticky sheet traps

Sticky sheets were used to validate the total insect abundance per night recorded by infrared interval photography. Here we made the assumption that the capture of insects by the sticky sheets did not interfere with the assessment of insect abundance by camera traps. Sticky sheets traps (Fentini Biocontrol, The Netherlands) were cut (18.5*25 cm) to fit in a frame to prevent bats accidentally touching it. Traps were placed on the lampposts at 30 cm below the luminaire

(Fig. 1a) between 20:00 and 22:00 and were collected between 07:00 and 09:00 the next morning, immediately placed in a plastic cover and frozen. All insects at both sides of the sheet were counted, with usage of a magnifying glass when needed.

2.4. *Bat activity*

Bat activity was assessed with omnidirectional microphones FG-23329 (Knowles Electronics, Itasca, IL, USA) powered with 12 V batteries and connected to a custom-made amplifier and filter unit. Microphones were placed at 2.07 to 2.52 m (average 2.35 m; standard deviation, s.d. 0.11) above the ground and 1.87 to 4.40 m (average 2.92 m; s.d. 0.70) from the lamppost depending on the vegetation surrounding the lamppost. Sound recordings were digitised with an Analog-Digital-Converter USB-6346 (DAQ) (National Instruments, TEX, USA) at a sampling rate of 300 kHz and 16-bit resolution. All recording parameters were controlled and set with the MALTA software (Microphone Array Localisation Tool for Animals, version 3.6, CAE Software & Systems, Germany), and all sound recordings were stored on Mini PCs (Gemini X, Beelink). Recordings are stored in 10-s files. Bat activity was continuously recorded from 15 min before sunset to 15 min after sunrise.

Species identification was performed using the Tadarida software (Bas et al., 2017, online repository: https://github.com/YvesBas, January 2021 version). As 93 % of the calls were attributable to synanthropic pipistrelle species, we limited our analyses to these species. A bat pass was defined as the occurrence of two or more echolocation calls of a pipistrelle during a 10-s file.

Bat feeding activity was measured by counting the number of feeding buzzes per night, which correspond to insect capture attempts and consist of rapid sequences of short, linear pulses with pulse intervals gradually decreasing (Griffin et al., 1960; Schnitzler and Kalko, 2001). Buzzes were detected using the bat sonotype classifier (online repository: https://github.com/YvesBas/Tadarida-C/tree/master/Sonotypes, November 2020 version) built by Roemer et al. (2021). Spectrograms of all detected buzzes were visually inspected to avoid false positives. A subsample was taken as well to check for false negatives. We used the 'buzz ratio' of feeding buzzes relative to the number of bat passes as a measure of bat feeding activity. A buzz ratio of one indicates that every bat pass contains a feeding buzz (Vaughan et al., 1997).

2.5. *Statistical analysis*

Analyses were carried out using the statistical software R (version 4.1.2, R Core Team, 2021).

2.5.1. *Insect abundance per night*

To test for the effect of the light treatment on the insect abundance per night (using camera traps data), a generalized mixed model (GLMM) with a negative binomial distribution was applied, using glmer.nb from lmer package (Bates et al., 2015). We included light treatment and mean air temperature per night as fixed factors in the model. We accounted for the hierarchical structure of the data by adding nested random effects of site and night to the model intercept. We subsequently compared models with and without the fixed effects using the R anova function (SI, Table S2). The emmeans function from the emmeans package (Lenth, 2023) was used to perform post hoc tests with a Bonferroni correction.

2.5.2. *Foraging activity per night*

As the buzz ratio is a proportion, we fitted a zero-inflated beta model (using glmmTMB from glmmTMB package, Brooks et al., 2017) with a beta-distribution (link = logit), and light treatment and log-transformed insect abundance as well as their interaction as explanatory variables. We accounted for the hierarchical structure of the data by adding nested random effects of site and night to the model intercept. The emtrends function from the emmeans package (Lenth, 2023) was used to estimate the slopes of the covariate trend for each light treatment.

2.5.3. *Temporal activity patterns*

As sunset and sunrise times changed throughout the data collection and as bat activity tends to line up with sunset and sunrise times (Erkert,

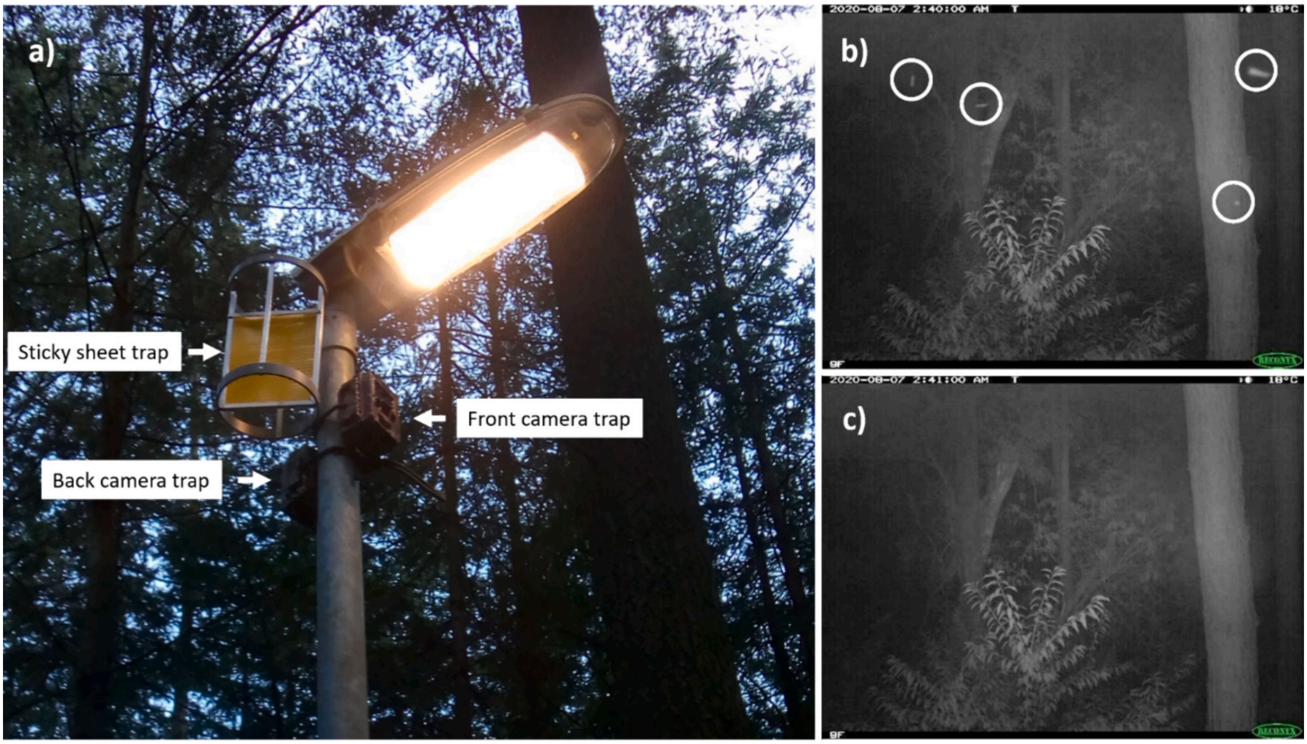

Fig. 1. Method to monitor insect abundance around experimental lampposts. a) Sticky sheet trap, front and back camera traps on a lamppost. b–c) Pictures captured by a camera trap at one-minute interval. b) Four insects are highlighted with a white circle. c) No insect was present.

1982), the time of observations were centred around the astronomical midnight of each recorded night using the sunTime function of the overlap package (Ridout and Linkie, 2009). We estimated temporal activity patterns using negative binomial generalized additive mixed-effect models (GAMMs) (gam function in the mgcv package (Wood, 2011)). The number of insect observations, bat passes and feeding buzzes per hour after sunset (relative to astronomical midnight) was used as the response variable. The light treatment and the hours after sunset were used as the predictor variables and the date as a random effect on the intercept to account for night-to-night variation in activity. Activity patterns were compared using plots of GAMM-predicted relative activity for each variable (insect abundance, number of bat passes and number of feeding buzzes).

3. Results

3.1. Insect abundance

Insect abundance as measured with sticky sheets and camera traps was positively correlated under red and white light ($R = 0.75; p < 0.001$ and $R = 0.77$; p < 0.001 respectively). However, the data from sticky sheets and camera traps were not correlated under the control dark treatment, with camera traps capturing more insects than sticky sheets ($R = 0.31; p = 0.245$).

Insect abundance as recorded by camera traps was significantly higher under the white treatment than under the other two light treatments and temperature did not have a significant effect on insect abundance (Fig. 2 and SI, Tables S3–S4).

3.2. Bat foraging activity

The number of bat passes and feeding buzzes per night was positively correlated for all light treatments ($R = 0.69; p = 0.001$ for dark, $R = 0.9$; p < 0.001 for red and $R = 0.78$; p < 0.001 for white).

When the insect abundance was low, the buzz ratio was low for all the light treatments, with about one feeding buzz for every 40 passes (Fig. 3). When insect abundance increased, the buzz ratio slightly increased under red light and at the control treatment, but it only increased significantly under white light (Table 1 and SI, Table S5). Thus, when prey availability was high, up to one pass out of four contained a feeding buzz at the white treatment, while bats tried to catch an insect every ten passes at the control and the red treatment (Fig. 3).

3.3. Activity patterns

Nightly insect abundance was greater only under white light ($Z = 6.039, p < 0.0001$ see SI Table S6). GAMMs showed a significant effect of time for each light treatment (SI, Table S6). Under dark natural conditions, insect abundance decreased throughout the night and did not show a bimodal activity pattern. Under red and white light, the number of insects per hour reached a maximum around four hours after sunset before gradually decreasing until sunrise (Fig. 4A).

The number of bat passes and feeding buzzes followed similar temporal patterns under the same light conditions. In unlit conditions, pipistrelles exhibited activity peaks after sunset and before sunrise (Fig. 4B and C). The hourly number of bat passes also showed a slight increase around midnight (Fig. 4B). Under red light, the activity remained constant throughout the night (passes: $\chi^2 = 2.606, p = 0.107$; feeding buzzes: $\chi^2 = 2.736, p = 0.101$, see SI, Tables S7 and S8). Under white light, the hourly number of bat passes and feeding buzzes reached a plateau between three hours and eight hours after sunset, before decreasing until sunrise (Fig. 4B and C).

4. Discussion

We showed that the insect abundance is higher in lit conditions and that their natural activity pattern is disrupted by ALAN. Similarly, light-tolerant pipistrelles are more active throughout the night in lit conditions and their foraging activity pattern is also altered compared to dark natural conditions. Overall, natural activity patterns are less impaired by red light than white light.

4.1. Insect abundance

Our results showed that ALAN increases insect abundance in forest edge habitat, but the effect varies according to the light spectrum. Shorter wavelengths of the white light treatment are more attractive for aerial insects than red light (Donners et al., 2018). Here we found a similar pattern per night in insect abundance using sticky sheets and camera traps, except at the dark control. ALAN may alter the insects' spatial distribution with more insects getting closer to lampposts (Russo et al., 2019) and thus getting captured both by camera traps and sticky sheets, while insects at the dark control are evenly spatially distributed and thus being more captured by camera traps than sticky sheets.

The insect size and the distance to the camera also introduce a bias in

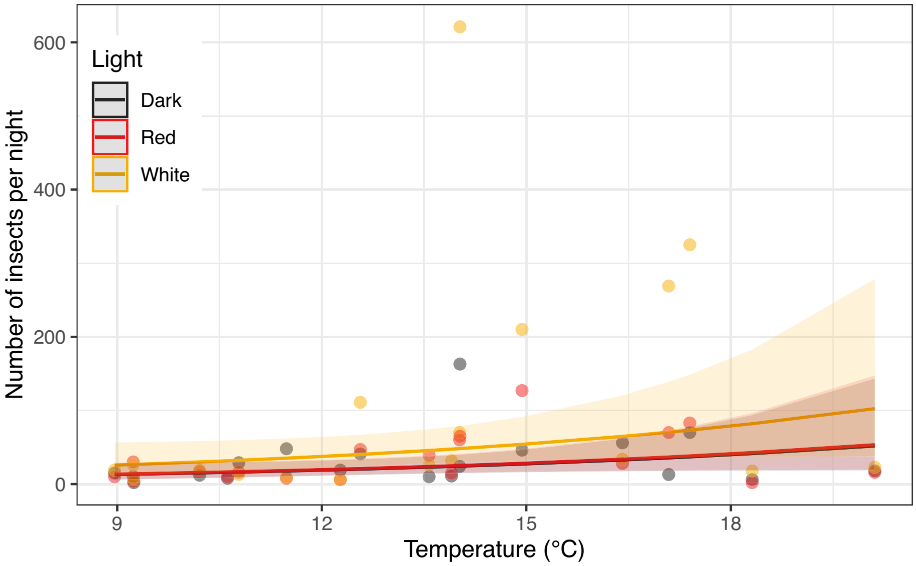

Fig. 2. Insect abundance (predicted lines from a statistical model with 95 % confidence intervals) in response to light treatment and air temperature for camera trap data. Dots represent the raw data.

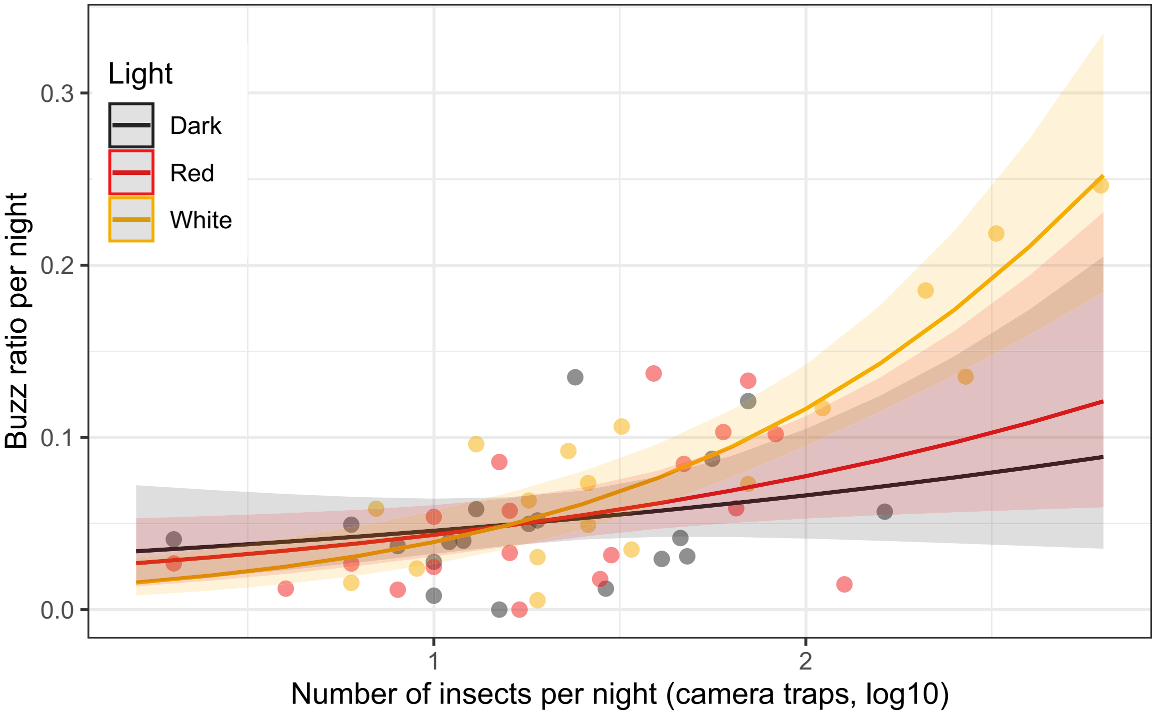

Fig. 3. Buzz ratio per night (predicted lines from a statistical model with 95 % confidence intervals) in response to the insect abundance per night for each light treatment. Dots represent the raw data.

Table 1
Estimates of slopes of the covariate trend for each light treatment based on the buzz ratio model.

Light	Insects (log) trend	SE	df	Lower confidence limit	Upper confidence limit
Dark	0.393	0.330	47	−0.2713	1.06
Red	0.617	0.271	47	0.0719	1.16
White	1.173	0.188	47	0.7959	1.55

insect detection (Ruczyński et al., 2020); the IR interval photography works well for larger insects such as macro moth species, where small dipterans may go undetected except when flying very close to the camera. This bias is important to consider when studying food availability for bats, as different bat species prey upon other types of insects. For example, *P. pipistrellus* generally feeds mostly on flies (Diptera) with wingspans of 5 mm or more (Swift et al., 1985). However, some studies reported already changes in diet preferences in several bat species, including *P. pipistrellus* which also feed on Lepidoptera (Arlettaz et al., 2000; Rydell, 1992). As ALAN alters the assemblage compositions of invertebrates (Grubisic and van Grunsven, 2021; Hakbong et al., 2021; Russo et al., 2019), this could lead to cascading effects on the diet preferences of bats.

As we cannot identify individuals, both for bats and insects, only the global activity for both taxa can be estimated. Furthermore, it is not possible to clearly identify insects on camera traps images as it would be with sticky sheets. Thus, we only took into account the number of insects and not the species groups to keep a global quantitative approach for both methods.

4.2. Bat foraging activity

White light attracts more insects and thus provides predictable foraging opportunities for bats (Prat and Yovel, 2020). However, bats optimize foraging rate according to a cost/benefit trade-off, which depends on the bat's ability to detect and catch prey and the risk of predation due to light (Jones and Rydell, 1994). In this study the buzz ratio drastically increased under white light compared to the dark situation or under red light when insects were present in larger numbers. This means that pipistrelles have more feeding opportunities in lit conditions with higher insect densities, with foraging benefits outweighing the potential increase in predation risk by visually-oriented predators like owls (Lesiński et al., 2009; Rosina and Shokhrin, 2011; Speakman, 1991). However, in previous studies, pipistrelles did not produce more buzzes in lit conditions along waterways or with increased moth availability (Charbonnier et al., 2014; Hooker et al., 2022). Therefore, bats' foraging response to ALAN and insect abundance is context-dependent. Some previous studies used bat passes as an estimator of foraging activity, as the number of feeding buzzes is often correlated with the number of bat passes (Mariton et al., 2022). In this study we however showed an interaction effect of ALAN and insect abundance on the buzz ratio, indicating that other parameters might alter the correlation between bat passes and feeding buzzes.

4.3. Temporal activity patterns

Both insects and bats (passes and feeding buzzes) displayed comparable temporal patterns under natural dark conditions with more activity after sunset, which is consistent with previous observations (Erkert, 1982; Mariton et al., 2023; O'Farrell and Bradley, 1970; Racey and Swift, 1985; Rydell et al., 1996; Swift, 1980). While bats exhibited a bimodal activity pattern in unlit conditions, the second peak before sunrise was not detectable for insects in our study. In lit conditions, the insect activity peak shifted to later in the night although it stayed before midnight. The nightly activity of pipistrelles increased under red light compared to unlit conditions, but remained constant throughout the night. This effect was stronger under white light, especially between three and eight hours after sunset. Therefore, bat activity is closely related to the diel activity pattern of their prey, but they also continue to forage during the second half of the night while the insect abundance gradually decreases under lit conditions, thus taking advantage of food availability as much as possible.

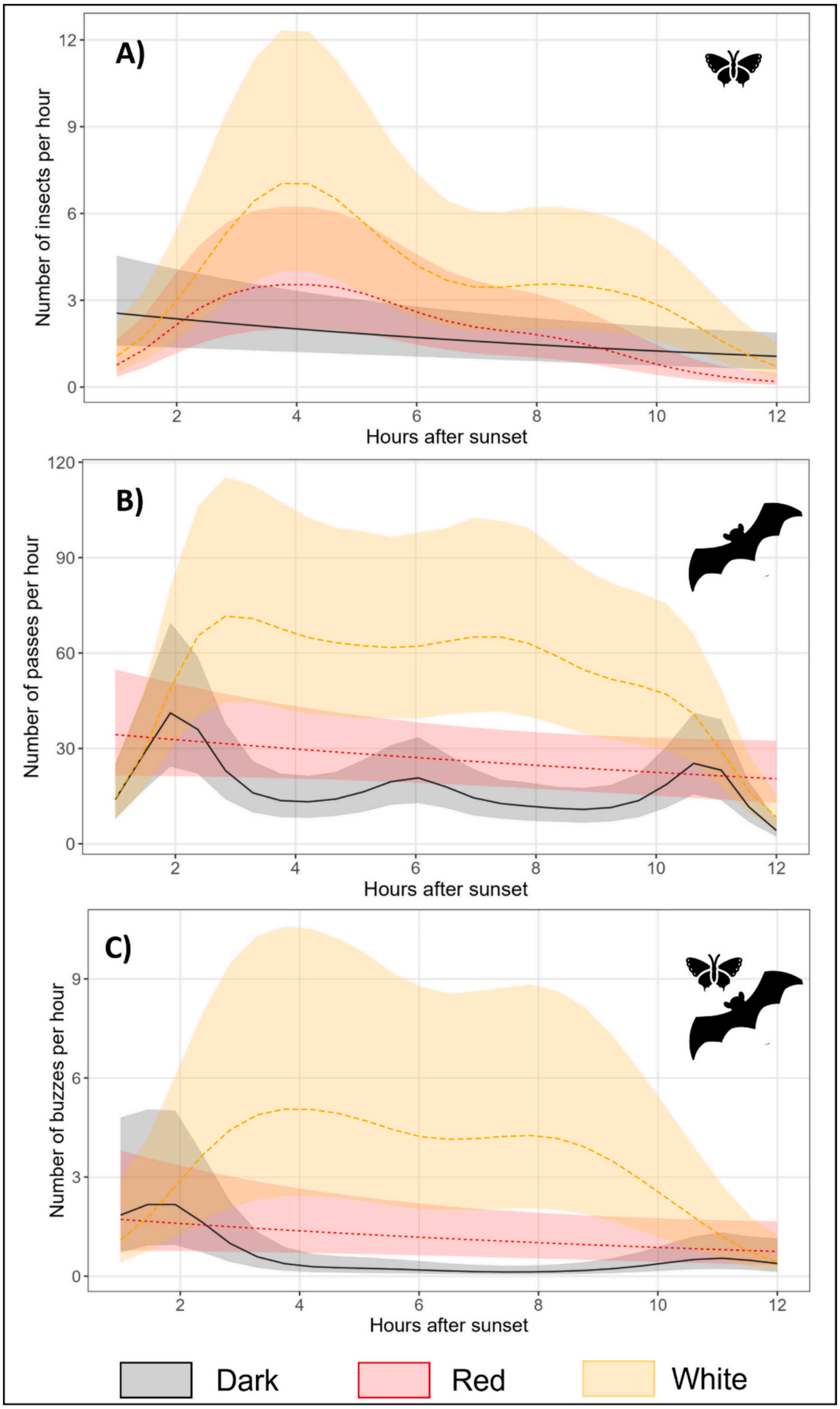

Fig. 4. Temporal distribution of A) insect abundance, B) bat passes and C) bat feeding buzzes throughout the night with 95 % confidence intervals. The time of each observation was centered to the astronomical midnight. 6 and 12 h after sunset correspond to midnight and sunrise, respectively.

The activity expansion throughout the night in lit conditions may have short-term benefits for the few light-tolerant bat species by providing a selective advantage of matching their activity pattern to that of their prey (Erkert, 1982). Artificial light could then alter community dynamics, for example in competition patterns, even between potentially competing pipistrelle species (Salinas-Ramos et al., 2021). The activity expansion could also lead in overexploitation of their food resources, or they could be exposed to new predators (Tougeron and Sanders, 2023). Thus, this could lead to population decline in the long term for pipistrelles, but also lead to cascading effects across their food web. These changes might also be detrimental for light-averse species (i.e. *Myotis* spp.), as pipistrelles are dominant, and dark areas are lacking food because insects agglomerate around the lights. Our results also show that natural diel activity pattern of insects and bats is less disrupted under red light than white light, thus opening the possibility of using spectral composition as a mitigation measure. Some previous studies already showed that red light is less harmful than other light spectra, especially for light-averse species (Spoelstra et al., 2017; Zeale et al., 2018). Using red light reduces the local benefit for opportunistic bats to forage on insects around light sources, and leaves the possibility for light-averse bats to forage there as well.

5. Conclusions

ALAN drives diel activity pattern of nocturnal aerial insects, and insect presence is a key driver for bat activity. Therefore, the advantage of the presence of light for synanthropic bats may be strongly determined by the continuous provision of insects throughout the night. Although light may be detrimental on a wider scale for both synanthropic and light-shy bats, the temporal effects of insect availability are an important factor behind the local advantage in foraging opportunities for synanthropic bat species.

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CRediT authorship contribution statement

Claire Hermans: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Iryna Litovska:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Mélyssa de Pastors:** Writing – review & editing, Investigation, Formal analysis. **Marcel E. Visser:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Kamiel Spoelstra:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Availability of data and materials

All data used in this study are available from the Dataverse Digital Depository, and can be accessed on request via the link: doi:10.34894/Z6PAIA.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.173699.

References

Arlettaz, R., Godat, S., Meyer, H., 2000. Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). Biol. Conserv. 93, 55–60. https://doi.org/10.1016/S0006-3207(99)00112-3.

Azam, C., Kerbiriou, C., Vernet, A., Julien, J.-F., Bas, Y., Plichard, L., Maratrat, J., Le Viol, I., 2015. Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? Glob. Chang. Biol. 21, 4333–4341. https://doi.org/10.1111/gcb.13036.

Bas, Y., Bas, D., Julien, J.-F., 2017. Tadarida: a toolbox for animal detection on acoustic recordings. Journal of Open Research Software 5, 6. https://doi.org/10.5334/jors.154.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bolliger, J., Collet, M., Hohl, M., Obrist, M.K., 2020a. Automated flight-interception traps for interval sampling of insects. PLoS One 15, e0229476. https://doi.org/10.1371/journal.pone.0229476.

Bolliger, J., Hennet, T., Wermelinger, B., Bösch, R., Pazur, R., Blum, S., Haller, J., Obrist, M.K., 2020b. Effects of traffic-regulated street lighting on nocturnal insect abundance and bat activity. Basic and Applied Ecology 47, 44–56. https://doi.org/10.1016/j.baae.2020.06.003.

Brooks, M.E., Kristensen, K., Benthem, K.J. van, Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9, 378–400. https://doi.org/10.32614/RJ-2017-066.

Charbonnier, Y., Barbaro, L., Theillout, A., Jactel, H., 2014. Numerical and functional responses of forest bats to a major insect pest in pine plantations. PLoS One 9, e109488. https://doi.org/10.1371/journal.pone.0109488.

Ciechanowski, M., Zając, T., Biłas, A., Dunajski, R., 2009. Nathusius' pipistrelles *Pipistrellus nathusii* (Chiroptera) reveal different temporal activity patterns in wooded and open riparian sites. Mammalia 73, 105–109. https://doi.org/10.1515/MAMM.2009.027.

Donners, M., van Grunsven, R.H.A., Groenendijk, D., van Langevelde, F., Bikker, J.W., Longcore, T., Veenendaal, E., 2018. Colors of attraction: modeling insect flight to light behavior. Journal of Experimental Zoology Part A: Ecological and Integrative Physiology 329, 434–440. https://doi.org/10.1002/jez.2188.

Eisenbeis, G., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, Washington DC, USA, pp. 191–198.

Erkert, H.G., 1982. Ecological aspects of bat activity rhythms. In: Kunz, T.H. (Ed.), Ecology of Bats. Springer US, Boston, MA, pp. 201–242. https://doi.org/10.1007/978-1-4613-3421-7_5.

Falchi, F., Bará, S., 2023. Light pollution is skyrocketing. Science 379, 234–235. https://doi.org/10.1126/science.adf4952.

Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C.C.M., Elvidge, C.D., Baugh, K., Portnov, B. A., Rybnikova, N.A., Furgoni, R., 2016. The new world atlas of artificial night sky brightness. Sci. Adv. 2, e1600377 https://doi.org/10.1126/sciadv.1600377.

Froidevaux, J.S.P., Fialas, P.C., Jones, G., 2018. Catching insects while recording bats: impacts of light trapping on acoustic sampling. Remote Sensing in Ecology and Conservation 4, 240–247. https://doi.org/10.1002/rse2.71.

Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal: nighttime light pollution. Biol. Rev. 88, 912–927. https://doi.org/10.1111/brv.12036.

Griffin, D.R., Webster, F.A., Michael, C.R., 1960. The echolocation of flying insects by bats. Anim. Behav. 8, 141–154. https://doi.org/10.1016/0003-3472(60)90022-1.

Grubisic, M., van Grunsven, R.H., 2021. Artificial light at night disrupts species interactions and changes insect communities. Current Opinion in Insect Science 47, 136–141. https://doi.org/10.1016/j.cois.2021.06.007.

Hakbong, L., Yong-Chan, C., Sang-Woo, J., Yoon-Ho, K., Seung-Gyu, L., 2021. Changes in nocturnal insect communities in forest-dominated landscape relevant to artificial light intensity. J. Ecol. Environ. 45, 24. https://doi.org/10.1186/s41610-021-00207-9.

Hayes, J.P., 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. J. Mammal. 78, 514–524. https://doi.org/10.2307/1382902.

Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: impacts of a current mitigation strategy on riparian bats. Environ. Pollut. 307, 119552 https://doi.org/10.1016/j.envpol.2022.119552.

Johnson, C.G., 1950. A suction trap for small airborne insects which automatically segregates the catch into hourly samples. Ann. Appl. Biol. 37, 80–91. https://doi.org/10.1111/j.1744-7348.1950.tb00952.x.

Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 346, 445–455. https://doi.org/10.1098/rstb.1994.0161.

Kunz, T.H., 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. J. Mammal. 54, 14–32. https://doi.org/10.2307/1378869.

Kyba, C.C.M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C.D., Gaston, K.J., Guanter, L., 2017. Artificially lit surface of Earth at night increasing in radiance and extent. Sci. Adv. 3, e1701528 https://doi.org/10.1126/sciadv.1701528.

Kyba, C.C.M., Altıntaş, Y.Ö., Walker, C.E., Newhouse, M., 2023. Citizen scientists report global rapid reductions in the visibility of stars from 2011 to 2022. Science 379, 265–268. https://doi.org/10.1126/science.abq7781.

Lenth, R.V., 2023. emmeans: Estimated Marginal Means, aka Least-squares Means.

Lesiński, G., Gryz, J., Kowalski, M., 2009. Bat predation by tawny owls *Strix aluco* in differently human-transformed habitats. Ital. J. Zool. 76, 415–421. https://doi.org/10.1080/11250000802589535.

Mariton, L., Kerbiriou, C., Bas, Y., Zanda, B., Le Viol, I., 2022. Even low light pollution levels affect the spatial distribution and timing of activity of a "light tolerant" bat species. Environ. Pollut. 305, 119267 https://doi.org/10.1016/j.envpol.2022.119267.

Mariton, L., Le Viol, I., Bas, Y., Kerbiriou, C., 2023. Characterising diel activity patterns to design conservation measures: case study of European bat species. Biol. Conserv. 277, 109852 https://doi.org/10.1016/j.biocon.2022.109852.

O'Farrell, M.J., Bradley, W.G., 1970. Activity patterns of bats over a desert spring. J. Mammal. 51, 18–26. https://doi.org/10.2307/1378527.

Owens, A.C.S., Lewis, S.M., 2022. Artificial light impacts the mate success of female fireflies. R. Soc. Open Sci. 9, 220468 https://doi.org/10.1098/rsos.220468.

Prat, Y., Yovel, Y., 2020. Decision making in foraging bats. Curr. Opin. Neurobiol. 60, 169–175. https://doi.org/10.1016/j.conb.2019.12.006.

R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from. https://www.R-project.org.

Racey, P.A., Swift, S.M., 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. J. Anim. Ecol. 54, 205–211. https://doi.org/10.2307/4631.

Rachwald, A., 1992. Habitat preference and activity of the noctule bat *Nyctalus noctula* in the Białowieża Primeval Forest. Acta Theriol. 37, 413–422. https://doi.org/10.4098/AT.arch.92-42.

Reconyx, I., 2016. Reconyx MapView Professional Software.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337. https://doi.org/10.1198/jabes.2009.08038.

Roemer, C., Julien, J.-F., Bas, Y., 2021. An automatic classifier of bat sonotypes around the world. Methods Ecol. Evol. 12, 2432–2444. https://doi.org/10.1111/2041-210X.13721.

Rosina, V.V., Shokhrin, V.P., 2011. Bats in the diet of owls from the Russian Far East, southern Sikhote Alin. Hystrix, the Italian Journal of Mammalogy 22, 205–213. https://doi.org/10.4404/hystrix-22.1-4503.

Rowse, E.G., Harris, S., Jones, G., 2018. Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats. R. Soc. Open Sci. 5, 180205 https://doi.org/10.1098/rsos.180205.

Ruczyński, I., Hałat, Z., Zegarek, M., Borowik, T., Dechmann, D.K.N., 2020. Camera transects as a method to monitor high temporal and spatial ephemerality of flying nocturnal insects. Methods Ecol. Evol. 11, 294–302. https://doi.org/10.1111/2041-210X.13339.

Russo, D., Cistrone, L., Garonna, A.P., Jones, G., 2011. The early bat catches the fly: daylight foraging in soprano pipistrelles. Mamm. Biol. 76, 87–89. https://doi.org/10.1016/j.mambio.2009.08.002.

Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P., Ancillotto, L., 2019. Artificial illumination near rivers may alter bat-insect trophic interactions. Environ. Pollut. 252, 1671–1677. https://doi.org/10.1016/j.envpol.2019.06.105.

Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. Funct. Ecol. 6, 744–750. https://doi.org/10.2307/2389972.

Rydell, J., Entwistle, A., Racey, P.A., 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. Oikos 76, 243–252. https://doi.org/10.2307/3546196.

Salinas-Ramos, V.B., Ancillotto, L., Cistrone, L., Nastasi, C., Bosso, L., Smeraldo, S., Sánchez Cordero, V., Russo, D., 2021. Artificial illumination influences niche segregation in bats. Environ. Pollut. 284, 117187 https://doi.org/10.1016/j.envpol.2021.117187.

Sanders, D., Frago, E., Kehoe, R., Patterson, C., Gaston, K.J., 2021. A meta-analysis of biological impacts of artificial light at night. Nature Ecology & Evolution 5, 74–81. https://doi.org/10.1038/s41559-020-01322-x.

Schnitzler, H.U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. BioScience 51, 557–569. https://doi.org/10.1641/0006-3568(2001)051[0557:EBIEB]2.0.CO;2.

Speakman, J.R., 1991. The impact of predation by birds on bat populations in the British Isles. Mammal Rev. 21, 123–142. https://doi.org/10.1111/j.1365-2907.1991.tb00114.x.

Speakman, J.R., Rydell, J., Webb, P.I., Hayes, J.P., Hays, G.C., Hulbert, I.A.R., McDevitt, R.M., 2000. Activity patterns of insectivorous bats and birds in northern Scandinavia (69° N), during continuous midsummer daylight. Oikos 88, 75–86. https://doi.org/10.1034/j.1600-0706.2000.880109.x.

Spoelstra, K., van Grunsven, R.H.A., Donners, M., Gienapp, P., Huigens, M.E., Slaterus, R., Berendse, F., Visser, M.E., Veenendaal, E., 2015. Experimental illumination of natural habitat—an experimental set-up to assess the direct and indirect ecological consequences of artificial light of different spectral composition. Philos. Trans. R. Soc. B 370, 20140129. https://doi.org/10.1098/rstb.2014.0129.

Spoelstra, K., van Grunsven, R.H.A., Ramakers, J.J.C., Ferguson, K.B., Raap, T., Donners, M., Veenendaal, E.M., Visser, M.E., 2017. Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. Proc. R. Soc. B Biol. Sci. 284, 20170075 https://doi.org/10.1098/rspb.2017.0075.

Swift, S.M., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. J. Zool. 190, 285–295. https://doi.org/10.1111/j.1469-7998.1980.tb01428.x.

Swift, S.M., Racey, P.A., Avery, M.I., 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. The Journal of Animal Ecology 54, 217–225. https://doi.org/10.2307/4632.

Tougeron, K., Sanders, D., 2023. Combined light pollution and night warming as a novel threat to ecosystems. Trends Ecol. Evol. 38, 701–704. https://doi.org/10.1016/j.tree.2023.05.012.

van Grunsven, R.H.A., van Deijk, J.R., Donners, M., Berendse, F., Visser, M.E., Veenendaal, E., Spoelstra, K., 2020. Experimental light at night has a negative long-term impact on macro-moth populations. Curr. Biol. 30, R694–R695. https://doi.org/10.1016/j.cub.2020.04.083.

van Langevelde, F., van Grunsven, R.H.A., Veenendaal, E.M., Fijen, T.P.M., 2017. Artificial night lighting inhibits feeding in moths. Biol. Lett. 13, 20160874 https://doi.org/10.1098/rsbl.2016.0874.

Vaughan, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. J. Appl. Ecol. 34, 716–730. https://doi.org/10.2307/2404918.

Wood, S.N., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models: estimation of semiparametric generalized linear models. J. R. Stat. Soc. Ser. B Stat Methodol. 73, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x.

Zeale, M.R.K., Stone, E.L., Zeale, E., Browne, W.J., Harris, S., Jones, G., 2018. Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats. Glob. Chang. Biol. 24, 5909–5918. https://doi.org/10.1111/gcb.14462.