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Artificial light at night (ALAN) pollution alters bat lunar chronobiology: insights from broad-scale long-term acoustic monitoring

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Abstract

Background The timing of behavior and habitat use of nocturnal animals can be influenced by the lunar cycle in nature. The prevalence of artificial light at night (ALAN) has been recognized as a source of environmental pollution. The interaction between ALAN and the lunar cycle on bat behavior is important for understanding anthropogenic effects on bats. We utilized a decade (2012–2022) of acoustic monitoring data collected in North Carolina, United States, to investigate the relationship between bat activity, lunar cycle, and light pollution. We examined whether the amount of lunar illumination affected species-specific nightly activity and whether hourly bat activity patterns varied between nights with different moon phases. We further investigated if the relationship between bat activity and the lunar cycle might be altered by light pollution.

Results We found that seven bat species showed activity variation across nights in relation to the amount of moon illumination when ALAN was absent. In general, bats were less active on full moon nights compared to new moon nights. Light pollution interacted with the bat–lunar relationship in five of the seven species, masking the effect of the lunar cycle. We identified delayed bat activity patterns on nights with a full or waxing moon in seven species, and light pollution altered that pattern in four species. Overall, ALAN was associated with decreased bat activity independent of lunar cycle effects.

Conclusions Our study demonstrated that at a broad spatial scale, ALAN negatively affected many North American temperate bat species and altered their lunar chronobiology. As light pollution is spreading to historically dark areas and habitats, ALAN might couple with other threats, such as the white-nose syndrome or climate change, to cause cascading damage in the environment that depends on ecosystem services such as pest control provided by bats. We argue that further research and conservation actions are needed to mitigate the impact of light pollution.

Keywords Artificial light at night, ALAN, Bats, Chiroptera, Chronobiology, Light pollution, Lunar cycle, Moonlight

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Background

Artificial light at night (ALAN) is a form of pollution associated with the unintentional and obstructive illumination of the environment by artificial light sources during the night to extend safety and productivity to humans (Olsen et al. 2014; Gallaway et al. 2010; Hölker et al. 2010). ALAN increases to as much as 20% annually in North America due to urbanization (Hölker et al. 2010). The scale of light pollution fluctuates depending on location as urban areas are known to have increased incidence of light pollution compared to rural areas (Pun et al. 2014). Natural environments have approximately 0.1–0.3 lux illuminance on a night with a full moon. In contrast artificial light produced from a shopping mall is about 200 times more than a full moon night at about 20–30 lux (Falchi et al. 2011). Regardless of location, a variety of aspects of wildlife such as reproductive cycle, inter/intraspecies communication, spatial orientation, and migration are impacted by ALAN (Bobkowska et al. 2016; Hölker et al. 2010).

For nocturnal animals, the timing of behavior and habitat use depends on the cue of moonlight in the natural environment (Kronfeld-Schor et al. 2013). The moon's illumination changes during the monthly lunar cycle and the amount of light available varies significantly depending on the moon phase (Ignatavičius et al. 2021). Numerous wildlife species respond to fluctuation of light levels throughout the lunar cycle, from full moon to new moon (Murugavel et al. 2021). An increase in moonlight may cause nocturnal prey species to become more visible to their predators (Prugh and Golden 2014; Kronfeld-Schor et al. 2013). Species that primarily use senses other than vision (such as olfaction, echolocation, commonly found in rodents, bats, carnivores) are more likely to avoid open habitats and have suppressed activity by increased lunar illumination than those that primarily use vision to avoid their predators (Prugh and Golden 2014).

Bats may respond to moonlight variation, indicated by the negative correlation between bat activity and moonlight intensity (a phenomenon known as lunar-phobia, Prugh and Golden 2014; Saldaña-Vázquez and Munguía-Rosas 2013). Such correlations have been explained by predation risk or availability of prey (Lang et al. 2006; Prugh and Golden 2014). For example, Lang et al. (2006) found that an insectivorous bat *Lophostoma silvicolum* (white-throated round-eared bat) reduced its activity during bright nights due to the lack of insect prey. Further, studies have found that some species exhibit lunar-phobia while others are lunar-philic in the same area due to ecological niche partitioning (Appel et al. 2017, 2019; Gomes et al. 2020). Adjustment of habitat use has also been found in bats responding to resource fluctuations

during lunar cycles (Brack and LaVal 1985; Hecker and Brigham 1999; Roeleke et al. 2018).

ALAN has much higher light intensity than natural moonlight by one or two orders of magnitude (Falchi et al. 2011; Davies et al. 2013). Therefore, the response of bats to the lunar cycle could be masked by ALAN. ALAN itself might be beneficial to certain bat species as certain wavelengths of light attract several species of insect prey (Van Langevelde et al. 2011; Li and Wilkins 2022; Russo et al. 2019). In addition, ALAN has been shown to affect foraging success of insectivorous bats by interfering with insects' defense mechanisms, whereby bats such as Cape serotine bats (*Neoromicia capensis*) in unlit areas have reduced moth consumption compared to bats in artificially lit areas (Minnaar et al. 2015). Negative effects of ALAN on certain bat species have also been documented (Barré et al. 2021; Luo et al. 2021; Voigt et al. 2021), including some North American species such as the little brown bat (*Myotis lucifugus*, Seewagen and Adams 2021). Studies have found the importance of maintaining dark corridors for bats to commute (Zeale et al. 2018; Straka et al. 2019). At the community level, ALAN may interfere with competition dynamics between bat species and alter species natural habitat preferences (Salinas-Ramos et al. 2021). Despite the importance of both the lunar cycle and ALAN on bat behavior, it is not known how ALAN and the lunar cycle might interact to influence bat activity patterns.

We used four long-term bat acoustic monitoring data sets collected between 2012 and 2022 in North Carolina, United States, to investigate the relationship between bat activity, lunar cycle, and ALAN. Specifically, we aimed to address the following questions: first, independently whether the amount of moon illumination affected species-specific nightly activity and whether species-specific bat activity varied between sites with and without ALAN; second, whether the bat activity pattern within a night varied between full moon and new moon phases or between waxing and waning moon phases. Furthermore, we aimed to investigate if any bat lunar relationship might be altered due to ALAN. For the first question, we hypothesized that moon illumination would have no effect on species-specific bat activity, based on previous studies on the hoary bat (*Lasiurus cinereus*) and silver-haired bat (*Lasionycteris noctivagans*) where no effect of the lunar cycle was found (Hecker and Brigham 1999; Baerwald and Barclay 2011). We also hypothesized that ALAN would affect bat activity in a species-specific manner independently from moon illumination. Only certain species such as the Mexican free-tailed bat that were urban-adapted would have higher activities at sites with ALAN presence than sites without ALAN (Li and Wilkins 2022). For the second question, we hypothesized

that hourly bat activity within a night would show no difference among nights with different moon phases. Based on the meta-analysis (Saldaña-Vázquez and Munguía-Rosas 2013), we predicted that species that used canopies such as the eastern red bat (*Lasiurus borealis*) would display different hourly activity patterns between full moon and new moon nights and between waxing and waning nights. Lastly, we hypothesized that ALAN would mask any effect of the lunar cycle due to its strong illuminance (Falchi et al. 2011; Davies et al. 2013) and predicted that different patterns would be found between ALAN presence and absence sites.

Methods

Study area and bat monitoring sites

We used bat acoustic monitoring data collected between 2012 and 2022 in North Carolina, United States for this study. North Carolina is a state located in the southeastern United States with a temperate climate (Robinson 2015). There are three regions of North Carolina with distinct geologies and climates: mountains, piedmont, and coastal plain. The mountain region has low mean annual temperatures and is home to several national forests. The piedmont region is the most urbanized region with the most major cities (Li et al. 2019). The coastal plain is predominantly rural and agricultural and has a warmer climate than other regions (Parker et al. 2020; Grider et al. 2016). Since 2012, year-round remote bat acoustic monitoring sites have been gradually established across the states to collect baseline bat information (Grider et al. 2016; Parker et al. 2020).

In this study, we selected 15 sites (Fig. 1) that had at least two years of year-round bat monitoring data from

four existing long-term projects (site information in Additional file 1: Table S1). Even though sites included in this study were established for different studies by either the first or the last author, all of them were in forested areas with similar site characteristics featuring corridors or small openings described by Grider et al. (2016) and Parker et al. (2020). Some of the sites were monitored over a waterbody, which was recorded as a covariate for the statistical analysis. We also recorded site region as a covariate for the statistical analysis using the region classification described in Parker et al. (2020). At each site, either a Wildlife Acoustics SM2 bat detector (Wildlife Acoustics, Inc, Concord, Massachusetts, United States) or an AnaBat SD2 bat detector (Titley Scientific Inc., Australia) was used for acoustic monitoring. All detectors were placed about 3 m above the ground and set to record bat activity from sunset to sunrise nightly year-round. The specific detector setup is described by Grider et al. (2016) and Parker et al. (2020). The same brand/make of detectors was used at each site for the data used in this study. The detector brand/make was recorded as a covariate detector type for statistical analysis.

Bat acoustic recording analysis

For all bat acoustic recordings, we used Kaleidoscope (version 4.5, Wildlife Acoustics Inc., Maynard, MA, United States) to process files and automatically assign species identification. We only considered recording files that had at least three complete bat echolocation calls within 0.5 s for species identification (each qualified file as a bat pass) and discarded other files. In North Carolina, the following eight species have been found with statewide distributions (Li et al. 2019; Li and

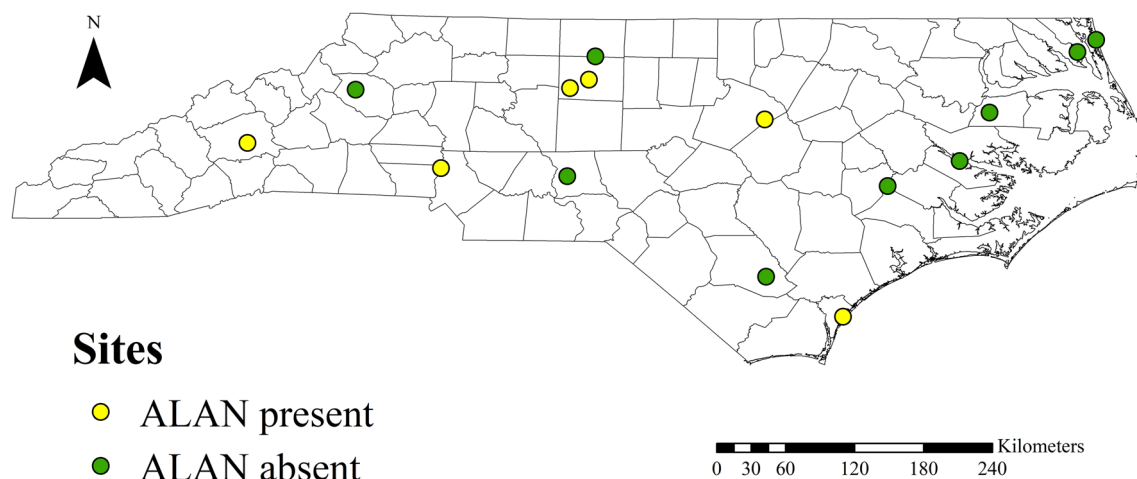


Fig. 1 Study sites in North Carolina, United States. All sites had at least 2 years of continuous nightly bat acoustic monitoring between 2012 and 2022. The artificial light at night (ALAN) condition of each site was determined by nighttime light data collected in 2012 and 2022 by the National Aeronautics and Space Administration

Kalcounis-Rueppell 2018): big brown bats (*Eptesicus fuscus*, EPFU), eastern red bats (*Lasiurus borealis*, LABO), hoary bats (*Lasiurus cinereus*, LACI), silver-haired bats (*Lasionycteris noctivagans*, LANO), little brown bat (*Myotis lucifugus*, MYLU), evening bats (*Nycticeius humeralis*, NYHU), tricolored bats (*Perimyotis subflavus*, PESU), and Mexican free-tailed bats (*Tadarida brasiliensis*, TABR). Thus, these species were selected as candidate species for acoustic analysis. In addition, in the mountain region there are records of gray bat (*Myotis grisescens*, MYGR), eastern small-footed myotis (*Myotis leibii*, MYLE), northern long-eared bat (*Myotis septentrionalis*, MYSE), and Indiana bat (*Myotis sodalis*, MYSO). These species were included as candidate species for the mountain region sites. For coastal plain sites, southeastern myotis (*Myotis austroriparius*, MYAU) and northern long-eared bat (*Myotis septentrionalis*, MYSE) were additionally included as candidate species. Although other bat species are present in North Carolina, they are rare and were not considered in the acoustic analysis.

After processing recording files in Kaleidoscope, the first author manually verified all bat passes that were identified as a species in the genus of *Myotis* by comparing recordings with voucher reference calls collected by either the first or the last author in other projects. We only confirmed a *Myotis* species presence when at least three different call passes on a night were verified to that species. For other species, we used the match ratio generated by Kaleidoscope for each bat pass to determine whether we accepted a species identification. We only considered a bat pass identified to species if the match ratio was greater than 0.60, which was a value essential for accurate identification in the study area after comparing Kaleidoscope automatic identification and manual identification based on previous work (Li and Kalcounis-Rueppell 2018; Schimpp et al. 2018). Because night length varies among seasons, we standardized species-specific bat activity by using the number of passes per hour. We also excluded any nights when the detector log files suggested that only a partial night was monitored (e.g., battery issue or memory card issue).

ALAN condition, weather, and moon phase data

To determine the ALAN condition at each site, we used nighttime light data from NASA (Román et al. 2018) directly on NASA Worldview (<https://worldview.earthdata.nasa.gov/>). We visually examined the site ALAN condition in 2012 and 2022 based on the site coordinates. Sites that were classified as ALAN present had radiance larger than $8 \text{ nW cm}^{-2} \text{ sr}^{-1}$, whereas ALAN absent sites had radiance less than $0.8 \text{ nW cm}^{-2} \text{ sr}^{-1}$. We also confirmed that no ALAN condition changes between 2012

and 2022 for all sites. In total, we had 6 ALAN present sites and 9 ALAN absent sites (Fig. 1).

For nights when bat acoustic recordings were collected, we followed the protocol described by Parker et al. (2020) to extract nightly weather data of temperature, wind speed, and sky condition from the weather underground network (www.wunderground.com). Because our goal was to investigate the effect of moonlight on bats, we used 'sky condition' in the weather data to exclude nights when the sky had clouds. Previous studies showed that both temperature and wind speed could potentially affect bat activity (Parker et al. 2020; Li et al. 2020). We conducted a multicollinearity test on temperature and wind speed and found they were correlated (variance inflation factor/VIF=7.8). Therefore, we included only temperature as a covariate in the statistical analysis.

For nights when the sky was clear and a complete night of bat acoustic recordings were collected, we used the specific date via R package lunar (Lazaridis 2022) to extract moon phase variables. We extracted the numeric moon phase as the percentage of moon illumination on a specified date (0% for the new moon to 100% for the full moon, variable name moon illumination). We also extracted the categorical moon phase: full moon, waxing, new moon, and waning, based on the percentage of moon illumination and the moon-rise time.

Statistical analysis

We used R (R Development Core Team, 2018, version 4.2.1) for all statistical analyses and data visualization. We used 0.05 as the statistical significance criterion for all statistical tests. To investigate the relationship between the amount of moon illumination, ALAN, and species-specific nightly activity, we constructed generalized linear mixed model (GLMM) with species-specific activity as the dependent variable, using a negative binomial distribution for over-dispersed data (Li and Kalcounis-Rueppell 2018). For all GLMMs, we included moon illumination, ALAN, and nightly temperature as independent variables as well as an interaction term between moon illumination and ALAN to investigate if ALAN might alter the bat activity-moon illumination relationship. Prior to the formal analysis, we conducted preliminary analyses to examine if detector type, site over waterbody, and site region had effects on bat activity. We only found detector and site region affected bat activity and thus included them as random effects in GLMMs. We were able to construct GLMMs for seven species: the big brown bat, eastern red bat, hoary bat, silver-haired bat, evening bat, tricolored bat, and Mexican free-tailed bat.

For three species with less common occurrence, the southeastern myotis, little brown bat, and northern

long-eared bat, we extracted nightly presence/no detection instead of bat activity as the independent variable. We constructed GLMMs with a binomial distribution to examine the relationship between presence probability and moon illumination/ALAN. For these GLMMs, we also included nightly temperature as a covariate, and detector type and region as random effect when applicable. In addition, we excluded sites where these species were never recorded in each respective model. R package lme4 was used for GLMM modeling (Bolker et al. 2009). To visualize GLMM results, we used R package ggplot2 to plot fitted GLMM trendlines and their 95% confidence interval.

To investigate how the bat activity pattern within a night varied between full vs. new moon or between waxing vs. waning moon, we divided a night into a first half and a second half based on the total night length. We counted the number of passes for each species in the first half of the night and second half of the night and calculated the proportions. We then conducted a Chi-squared test to determine if the proportion of bat passes between the first half and the second half of the night varied between full vs. new moon or between waning vs. waxing moon. We conducted the Chi-squared tests separately for ALAN present sites and ALAN absent sites. We used

the first and second halves instead of actual time of the night to investigate how bat activity patterns might vary within a night, because our data set included year round monitoring and the sunset time varied by several hours between seasons in our study area (Li et al. 2020).

Results

In total, we had 2429 recording nights with a cloudless sky, 956 recording nights at ALAN present sites and 1473 recording nights at ALAN absent sites. The most frequently recorded species was the eastern red bat, followed by the evening bat, silver-haired bat, tricolored bat, hoary bat, big brown bat, and Mexican free-tailed bat. All these common species were recorded at all 15 sites. The little brown bat was only recorded at 10 sites (2 ALAN present sites, 8 ALAN absent sites). The southeastern myotis was only recorded at 8 sites (2 ALAN present sites, 6 ALAN absent sites). The northern long-eared bat was only recorded at 5 ALAN absent sites on the coast plain of North Carolina, consistent with our understanding of the distribution of this species (Grider et al. 2016).

Of the ten species, only the northern long-eared bat, tricolored bat, and Mexican free-tailed bat showed no response to moon illumination (all $p > 0.05$, Table 1, Fig. 2), partially supporting our hypothesis that moon

Table 1 Generalized linear mixed model results (regression estimate \pm standard error on top, p value at bottom) for the relationships between species-specific bat activity/presence probability, moon illumination, and ALAN condition

Species	Moon illumination	ALAN	ALAN \times Moon illumination intersection	ALAN present Moon illumination	ALAN absent Moon illumination	Temperature
EPFU	0.743 \pm 0.378 0.049	0.871 \pm 0.278 0.002	-1.001 \pm 0.446 0.025	0.730 \pm 0.370 0.016	-0.275 \pm 0.246 0.264	0.027 \pm 0.009 0.002
LABO	-0.009 \pm 0.276 0.974	1.347 \pm 0.229 < 0.001	-0.864 \pm 0.335 0.009	0.144 \pm 0.223 0.519	-0.896 \pm 0.206 < 0.001	0.143 \pm 0.009 < 0.001
LACI	0.400 \pm 0.445 0.369	2.670 \pm 0.357 < 0.001	-3.236 \pm 0.590 < 0.001	0.576 \pm 0.340 0.090	-3.492 \pm 0.438 < 0.001	0.088 \pm 0.016 < 0.001
LANO	-0.431 \pm 0.220 0.024	1.959 \pm 0.221 < 0.001	N/A	N/A	N/A	0.045 \pm 0.014 0.001
MYAU	2.084 \pm 1.143 0.068	3.572 \pm 0.868 < 0.001	-2.679 \pm 1.175 0.023	2.000 \pm 1.117 0.073	-0.468 \pm 0.238 0.049	N/A
MYLU	0.517 \pm 0.220 0.019	1.767 \pm 0.360 < 0.001	N/A	N/A	N/A	0.022 \pm 0.010 0.020
MYSE	0.318 \pm 0.327 0.330	N/A	N/A	N/A	N/A	0.062 \pm 0.012 < 0.001
NYHU	0.004 \pm 0.259 0.987	0.776 \pm 0.234 < 0.001	-0.718 \pm 0.333 0.032	0.122 \pm 0.261 0.641	-0.699 \pm 0.194 < 0.001	0.144 \pm 0.010 < 0.001
PESU	-0.021 \pm 0.200 0.918	1.971 \pm 0.207 < 0.001	N/A	N/A	N/A	0.054 \pm 0.011 < 0.001
TABR	-0.207 \pm 0.255 0.415	-0.428 \pm 0.273 0.071	N/A	N/A	N/A	0.047 \pm 0.015 0.002

Species abbreviations are defined in the text

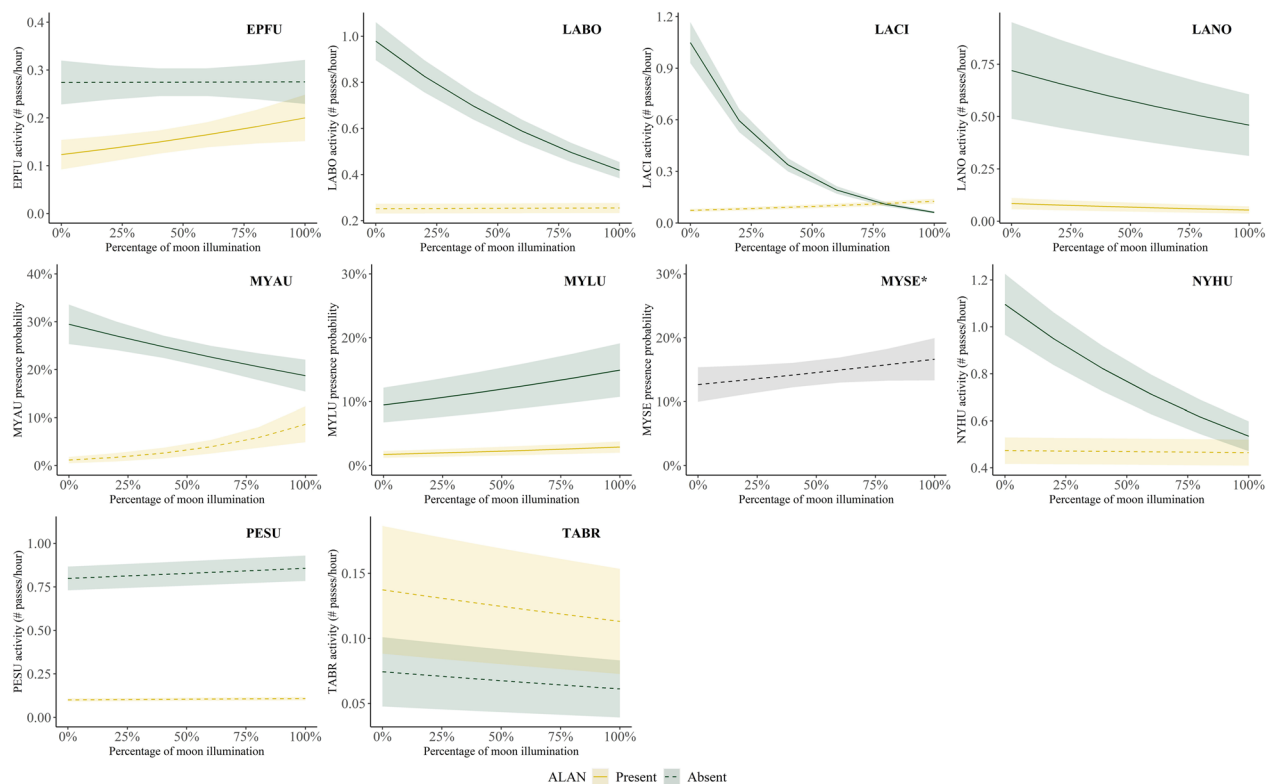


Fig. 2 Species-specific bat activity/presence probability across nights in relation to moon phase (indicated by percentage of moon illumination, 0% new moon, 100% full moon) estimated by generalized linear mixed effect models (GLMM) for ALAN present (yellow) and ALAN absent (green) sites. Significant relationships (GLMM regression coefficient $p < 0.05$) are illustrated by solid lines and nonsignificant relationships by dash lines. Species abbreviations are defined in the text. * Indicates that MYSE (northern long-eared bat) was only recorded at ALAN absent sites

illumination would have no effect on species-specific bat activity. For the tricolored bat and the Mexican free-tailed bat, no response to moon illumination was independent from the effect of ALAN (both interaction terms $p > 0.05$). Tricolored bat activity was approximately 4.0 times higher at ALAN absent sites than at ALAN present sites ($p < 0.001$, Fig. 2). For the Mexican free-tailed bat, no difference was found between ALAN present sites and absent site in terms of bat activity ($p = 0.071$, Fig. 2), rejecting our hypothesis on urban-adapted species being more active at ALAN presence sites. The silver-haired and the little brown bat responded to moon illumination independent of ALAN (both interaction terms $p > 0.05$), rejecting the hypothesis that moon illumination would have no effect on species-specific bat activity. Silver-haired bat activity decreased when moon illumination increased at both ALAN present and absent sites ($p = 0.045$, Table 1, Fig. 2). Silver-haired bat activity on average was approximately 2.5 times higher at ALAN absent sites than at ALAN present sites ($p < 0.001$, Fig. 2). The little brown bat responded positively to moon illumination ($p = 0.019$, Table 1, Fig. 2), which was the only species that showed a positive response regardless of ALAN.

On average, the chance of recording the little brown bat was approximately 5.2 times higher at ALAN absent sites than at ALAN present sites ($p < 0.001$, Fig. 2).

For the remaining five species, ALAN altered species responses to moon illumination (all interaction terms $p < 0.05$, Table 1), supporting the ALAN masking moon light hypothesis. The eastern red bat, hoary bat, southeastern myotis, and evening bat showed lunar phobia at ALAN absent sites (all $p < 0.05$, Table 1, Fig. 2). However, at ALAN present sites, none responded to moon illumination negatively (all $p > 0.05$, Table 1, Fig. 2). The big brown bat showed no response to moon illumination at ALAN absent sites. At ALAN present sites, big brown bat activity increased as moon illumination increased ($p = 0.016$, Table 1, Fig. 2). In general, the big brown bat, eastern red bat, hoary bat, and evening bat had higher activity at ALAN absent sites compared to ALAN present sites (1.9, 2.4, 2.2, 2.4 times higher respectively, all $p < 0.05$, Table 1, Fig. 2). The chance of recording the southeastern myotis was approximately 6.0 times higher at ALAN absent sites than at ALAN present sites.

In general, our hypothesis that hourly bat activity within a night would show no difference among nights

with different moon phases was rejected. When investigating how full vs. new moons affect bat activity patterns within a night, we found that ALAN absent sites saw proportionally more bat activity in the second half of the night on full moons than on new moons in all species investigated except for the big brown bat (eastern red bat $\chi^2=138.3$; hoary bat $\chi^2=56.7$; silver-haired bat $\chi^2=34.5$; evening bat $\chi^2=82.6$; tri-colored bat $\chi^2=20.8$; Mexican free-tailed bat $\chi^2=29.8$; all $p<0.001$; Fig. 3a), indicating delayed activity on full moon nights. At ALAN present sites, the delayed activity pattern was only found in the eastern red bat ($\chi^2=7.0$, $p=0.008$), silver-haired bat ($\chi^2=21.4$, $p<0.001$), evening bat ($\chi^2=122.3$, $p<0.001$), and Mexican free-tailed bat ($\chi^2=68.7$, $p<0.001$). The activity pattern within a night was not different between full and new moons for the hoary bat and the tri-colored bat at ALAN present sites (Fig. 3a).

When investigating how moon waning and waxing phases might affect bat activity patterns within a night,

we found differences in the big brown bat, evening bat, and tri-colored bat. For these species, ALAN absent sites saw proportionally more bat activity recorded in the second half of the night on waxing nights than on waning nights (big brown bat $\chi^2=148.5$, $p<0.001$; evening bat $\chi^2=155.5$, $p<0.001$; tri-colored bat $\chi^2=115.0$, $p<0.001$; Fig. 3b), indicating delayed activity on waxing nights. At ALAN bright sites, such pattern was only found in the tri-colored bats ($\chi^2=9.0$, $p=0.003$). There was no nightly activity pattern difference between waning and waxing nights in other species at ALAN present sites (Fig. 3b). These hourly activity pattern results suggested that the ALAN masking moonlight hypothesis was only supported by the hoary bat and the tri-colored bat between full and new moon nights as well as the big brown bat and the evening bat between waning and waxing moon nights.

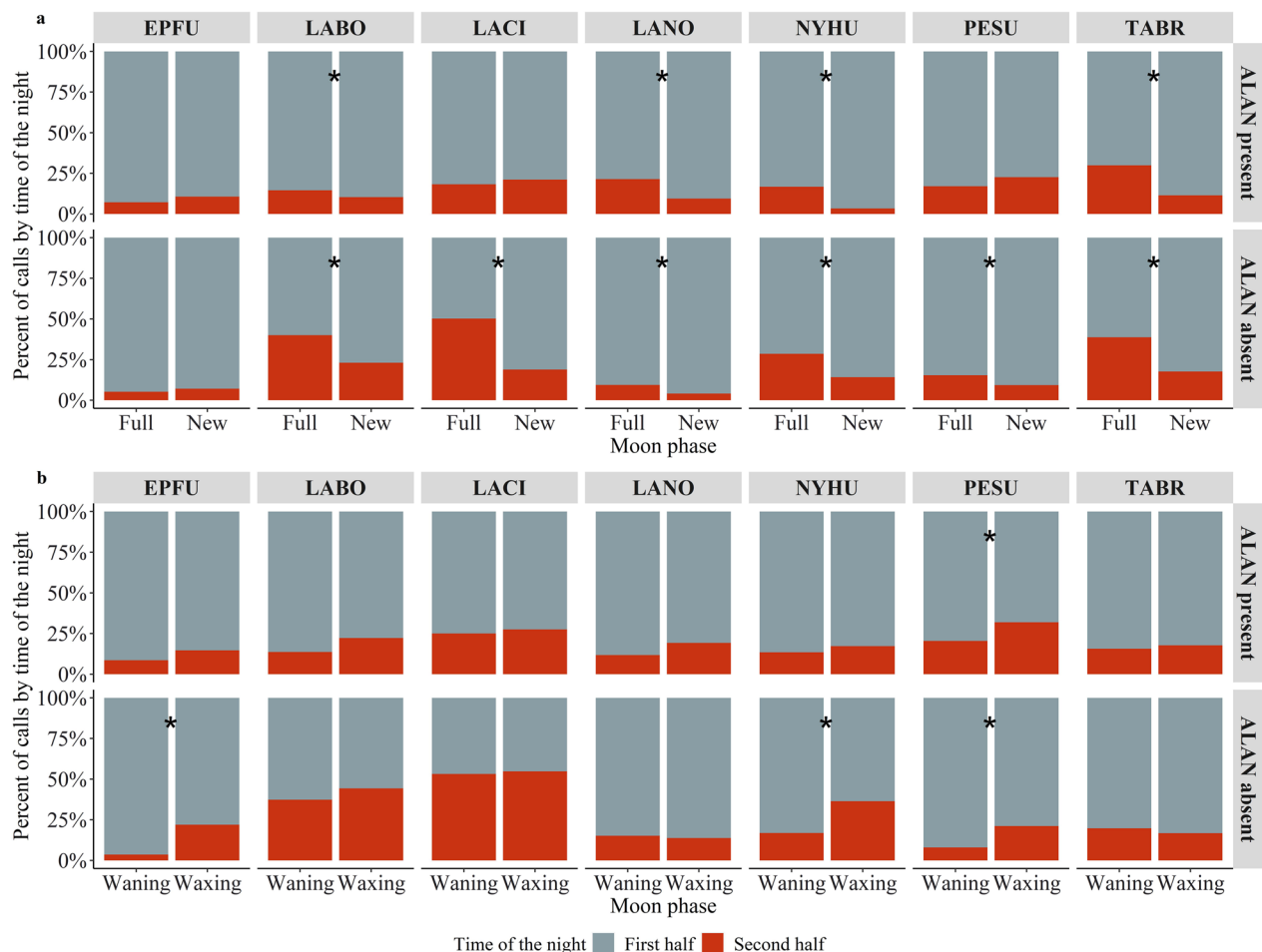


Fig. 3 Species-specific bat activity pattern within a night (percentage of activity in the first half of the night vs. the second half) compared between full moon vs. new moon and waxing moon vs. waning moon at ALAN present and ALAN absent sites. * Indicates activity pattern within a night varied significantly (Chi-squared tests, $p<0.05$) between moon phases. Species abbreviations are defined in the text

Discussion

Few studies have explicitly examined the effects of lunar cycle on temperate bats in North America (Hecker and Brigham 1999; Baerwald and Barclay 2011; Arndt et al. 2018; Negraeff and Brigham 1995; Whiting et al. 2021). Herein we not only examined lunar cycle, but also the effect and masking interaction of ALAN. We found that five bat species (eastern red bat, hoary bat, silver-haired bat, southeastern myotis, and evening bat) had lower acoustic activity when the amount of moon illumination increased in the environment without ALAN. Two of these species, the hoary bat and silver-haired bat, were examined in previous studies (Hecker and Brigham 1999; Baerwald and Barclay 2011). Contrary to our results, these studies did not find that the amount of moon illumination affected bat acoustic activity (Hecker and Brigham 1999; Baerwald and Barclay 2011) or emergence time (Arndt et al. 2018; Whiting et al. 2021). One major difference between our study and others is that we used data from year-round monitoring for over a decade whereas previous studies had only a few months of data, primarily in the summer. The difference in sampling scope might affect the ability to detect a quantitative pattern. In addition, our large data set allowed us to limit our investigation to nights with a cloudless sky, potentially removing the masking effect of clouds, which most previous studies did not do. Lastly, all previous studies examining the effects of moonlight on temperate bats in North America were conducted at more northern latitudes, and a global meta-analysis of bat lunar phobia suggests that lunar phobia is less likely to be detected as absolute latitude increases (Saldaña-Vázquez and Munguía-Rosas 2013).

The global meta-analysis also suggests that species-specific foraging habitat preferences can affect how bats respond to lunar cycles (Saldaña-Vázquez and Munguía-Rosas 2013). Bats foraging over water are more likely to be affected by moonlight due to high risks of being preyed upon (Saldaña-Vázquez and Munguía-Rosas 2013). Several of our long-term monitoring sites were established over water bodies (Parker et al. 2020), which might explain lunar phobia detected in our study. A few recent studies in South America also reported species-specific responses to lunar cycles (Appel et al. 2017, 2019; Vázquez et al. 2020; Gomes et al. 2020). Fast-flying species with long, narrow wings such as the Mexican free-tailed bat might be less likely to respond to lunar cycle than slow-flying species with short, broad wings due to the ability of escaping from predators (Appel et al. 2017, 2019; Vázquez et al. 2020). Our results on the Mexican free-tailed bat supported previous studies. However, our results on the hoary bat, an open space forager (Blakey et al. 2019), showed lunar phobia, which is contradictory

to existing knowledge that open space foraging species are not likely to respond to lunar cycle (Musila et al. 2019; Saldaña-Vázquez and Munguía-Rosas 2013). Such contradiction highlights the need to further investigate the mechanism of bats' responses to lunar cycle.

Regarding how bat activity patterns within a night varied with lunar cycle, we found that bat activity was delayed when more moonlight was present in the ALAN absent environment, which is consistent with previous studies (Appel et al. 2017; Vázquez et al. 2020). The eastern red bat, hoary bat, silver-haired bat, evening bat, tricolored bat, and Mexican free-tailed bat showed increased activity in the second half of the night on full moons when compared to new moons. The big brown bat, evening bat, and tricolored bat showed increased activity in the second half of the night on waxing moons compared to waning moons. These results support bat lunar phobia in the ALAN absent environment. Species-specific diel activity pattern has been recognized a long time ago and explained by niche partitioning (Kunz 1973). Recent studies found that such overnight patterns could be affected by urbanization and related anthropogenic disturbances (Schimpp et al. 2018; Li et al. 2020), which is one of the sources of ALAN.

The intensity of ALAN is at least 10 times stronger than the most intense moonlight and masks any effect of moonlight (Davies et al. 2013). To our knowledge, only one study (Mariton et al. 2022) has explicitly examined how bat activity patterns within a night differed among moon phases under the effects of light pollution. In our study, we found robust evidence of ALAN altering bat lunar relationships, masking the effects of lunar cycle on nightly and within-night bat activity patterns. Across nights, we found that the eastern red bat, hoary bat, southeastern myotis, and evening bat no longer responded to varying moonlight intensity with ALAN presence. We also found that the big brown bat showed an increase in activity at ALAN present sites as the moonlight intensity increased across nights. Within a night, the delayed activity pattern on full moon or waxing moon nights disappeared in the big brown bat, hoary bat, evening bat, and tri-colored bat when ALAN was present. This is consistent with the only study that showed ALAN masking the delaying effect of moonlight within a night in the Serotine bat (*Eptesicus serotinus*, Mariton et al. 2022).

Not all bat lunar relationships identified in our study were affected by ALAN. For nightly response to the amount of moon illumination, the silver-haired bat displayed lunar phobia independent from the ALAN condition. For the delayed activity within a night on a full or waxing moon, four species showed a delayed activity pattern at the ALAN present sites. The primary explanation

for bat lunar relationships is that moonlight could alter the perceived predation risk for bats, their prey, and their predators (Saldaña-Vázquez and Munguía-Rosas 2013; Lima and O’Keefe 2013). Several empirical studies have demonstrated how insects responded to lunar cycles thus affecting food availability for bats (Lang et al. 2006; Kolkert et al. 2020). However, studies on the activity in relation to moonlight of bats’ nighttime aerial predators, such as owls and other birds of prey, are still lacking. Furthermore, the underlying physiological and behavioral mechanism of bat lunar relationships is unclear. It is unknown whether bats use moonlight as a visual cue or a circadian clock is involved as suggested in other animals responding to lunar cycle (Kronfeld-Schor et al. 2013). Since we found varying effects of ALAN on bat lunar relationships, we speculate that different species might have different mechanisms for lunar cycle responses or that intrinsic mechanisms differentially interact with light levels. To investigate mechanisms, studies should use both field methods to monitor bat predators and laboratory methods to simulate light conditions (Tidau et al. 2022).

Independent from lunar chronobiology, our study also examined the effects of ALAN on bat acoustic activity. Nine out of ten species showed higher acoustic activity at the ALAN absent sites than at the ALAN present sites. The most extreme example is the northern long-eared bat, a forest interior species and slow flyer, which was never recorded at any ALAN bright sites. Only a few studies have examined the effect of ALAN on North American temperate bats. Two separate field experiments artificially lit naturally dark areas, and both found that big brown and little brown bats avoided lit sites (Seewagen and Adams 2021; Cravens and Boyles 2019). In addition, one of the studies also found the silver-haired bat to avoid lit sites (Seewagen and Adams 2021). No effect of ALAN was found on the eastern red bat, hoary bat, evening bat, or tricolored bat in these studies (Seewagen and Adams 2021; Cravens and Boyles 2019). In a study focusing on urban bats that might have somewhat adapted to ALAN in the city, scientists found that the big brown bat, eastern red bat, and silver-haired bat showed higher levels of activity at brighter sites in response to increased insect availability (Li and Wilkins 2022). However, their activity was still limited by the spatial clutter, which affected foraging habitat suitability (Li and Wilkins 2022).

No regional multiple-landscape scale study has explicitly examined the effect of ALAN across different light conditions on North American temperate bats. In general, ALAN is associated with urban environments (Davies et al. 2013; Falchi et al. 2011, 2016; Doll et al. 2006). Two regional multiple-landscape scale studies on

bats and urbanization showed that the big brown bat, silver-haired bat, and Mexican free-tailed bat had higher levels of activity as the degree of urbanization increased (Li and Kalcounis-Rueppell 2018; Li et al. 2019). However, both of those studies used the mobile transect survey technique to monitor bats right after sunset and did not compare the bat activity throughout a whole night. It is possible that urban dwelling bats were only active in the city immediately after sunset and would leave the city to forage in more natural conditions (Schimpp et al. 2018; Aguiar et al. 2021). Our results demonstrate that ALAN is likely to negatively affect bats at the regional multiple-landscape spatial scale and reduce habitat quality even for species that might be somewhat light tolerant, echoing recent findings on European bats (Russo et al. 2019; Mariton et al. 2022; Straka et al. 2021).

It is worth noting that we found the little brown bat to be lunar-philic regardless of the ALAN condition and the big brown bat to be lunar-philic at ALAN present sites. Similar lunar philia has been reported in South American bats, such as *Tadarida brasiliensis* in central Chile (Vásquez et al. 2020) and *Molossus molossus* in French Guiana (Gomes et al. 2020). We suspect that such results might come from interspecific competition among bats. In-flight social interactions, such as making competition warning calls has been documented in the big brown bat, evening bat, and Mexican free-tailed bat when multiple species were present at a quality foraging site (Springall et al. 2019). When a site changes from dark to bright temporarily due to the lunar cycle or permanently due to ALAN, the bat community structure might change accordingly by limiting light-sensitive species from accessing the site (Willems et al. 2022; Russo et al. 2019; Salinas-Ramos et al. 2021). Competitive interactions among bats should be emphasized in future studies on ALAN or lunar chronobiology.

We were unable to assess whether bats may have switched from echolocation to vision in the presence of light in our study. Using vision for foraging when sufficient illumination is available has been documented in bats (Eklöf and Jones 2003; Gutierrez et al. 2014; Danilovich et al. 2015). Bats may also be silent or reduce acoustic activity in other behavioral processes, since echolocation production is energy demanding (Currie et al. 2020; Corcoran et al. 2021). Our study used acoustic methods alone and therefore we cannot assess scenarios where bats alter their acoustic behaviors when light is present; rather we assume that lower calls mean less activity. Future studies should consider using other monitoring techniques such as video recording in combination with acoustic monitoring to investigate the effects of ALAN or lunar cycle on bats, ideally in a controlled experimental setting.

In the ALAN absent environment, any reduced bat foraging success (regardless of mechanism) on bright nights of full moon, can be compensated for by higher foraging activities on dark nights of new moon. In contrast, ALAN associated with human settlements is generally constant and relatively permanent. There is the need to further investigate the long-term physiological consequences of ALAN exposure and examine health conditions of ALAN impacted bats. As urbanization accelerates worldwide (United Nations 2019), conservation actions towards ALAN are needed. Efforts can be made to alter the ALAN spectrum (Lewanzik and Voigt 2017; Spoelstra et al. 2017) or improve urban forestry (Straka et al. 2019; Li et al. 2020). However, attention should also be paid to anthropogenic environments that are traditionally dark, such as agricultural lands.

Temperate bats provide tremendous benefits of ecosystem services via pest control in agricultural environments (Boyles et al. 2011). Due to climate change and socioeconomics, there is a trend of increased agricultural activities including harvesting, equipment transportation and setup, field prep and maintenance, irrigation, and pesticide applications at night. Even though there is no governmental data or scientific research to document how many growers have adopted nighttime farming, legislation has been made to require sufficient illumination for worker safety (e.g., DIR, California 2020). Such farming practices might change ALAN conditions in agricultural environments, reducing bat activity and ecosystem service in these areas.

Conclusions

Our study demonstrated that at a broad spatial scale, ALAN negatively affected the acoustic activity of many North American temperate bat species and altered their lunar chronobiology. Our evidence of temperate bat lunar chronobiology is established on data that spanned over a decade and covered a relatively large and geographically diverse area. Given the wide range of bat species negatively impacted by light pollution, we argue that further physiological research and conservation actions are needed. As the cost of illumination declines and the economic benefits of nighttime farming and other activities increase, light pollution is spreading to historically dark areas and habitats. ALAN might couple with other threats, such as the white-nose syndrome or climate change, to cause cascading damage in the environment that depends on ecosystem services provided by bats. We also want to emphasize the importance of long-term, year-round baseline bat acoustic monitoring. This type of data provides opportunities to address scientific questions that might otherwise remain unanswered.

Abbreviations

ALAN	Artificial light at night
GLMM	Generalized linear mixed model
EPFU	Big brown bats (<i>Eptesicus fuscus</i>)
LABO	Eastern red bats (<i>Lasiurus borealis</i>)
LACI	Hoary bats (<i>Lasiurus cinereus</i>)
LANO	Silver-haired bats (<i>Lasionycteris noctivagans</i>)
MYAU	Southeastern myotis (<i>Myotis austroriparius</i>)
MYGR	Gray bat (<i>Myotis grisescens</i>)
MYLE	Eastern small-footed myotis (<i>Myotis leibii</i>)
MYLU	Little brown bat (<i>Myotis lucifugus</i>)
MYSE	Northern long-eared bat (<i>Myotis septentrionalis</i>)
MYSO	Indiana bat (<i>Myotis sodalis</i>)
NYHU	Evening bats (<i>Nycticeius humeralis</i>)
PESU	Tricolored bats (<i>Perimyotis subflavus</i>)
TABR	Mexican free-tailed bats (<i>Tadarida brasiliensis</i>)

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00491-y>.

Additional file 1. Study site information.

Acknowledgements

Data used in the manuscript were previously collected independently for various projects with the support of the United States Fish and Wildlife Service, the North Carolina Wildlife Resources Commission, the University of North Carolina Greensboro, and Southeastern Bat Diversity Network, assisted by A. Matteson, A. Larson-Gray, K. King, C. Redd, K. Caldwell-Etchison, K. Clark, M. Liverman, C. Hickman, J. Costa, B. Cherry, C. Luckenbaugh, E. Corey, D. Fowler in the field. This manuscript was written as part of a special scientific reading and writing course supported by the University of North Carolina Greensboro Department of Biology, motivated by participation in the Council of Undergraduate Research (CUR) Transformation Project, for which we thank gratefully. We also appreciate the thoughtful comments of two anonymous reviewers that improved the presentation of this work.

Author contributions

HL: conceptualization, methodology, software, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, visualization, supervision, project administration, funding acquisition; PA, SB SL, JL, CM, PM, CN, CT, MT, NLW: conceptualization, investigation, data curation, writing—original draft preparation, writing—review and editing; JFG, KAP: investigation, data curation, writing—review and editing, funding acquisition; MCKR: writing—review and editing, supervision, project administration, funding acquisition.

Funding

Data used in the manuscript were previously collected independently for various projects with the support of the United States Fish and Wildlife Service, the North Carolina Wildlife Resources Commission, the University of North Carolina Greensboro, and Southeastern Bat Diversity Network. No direct funding was received for the reported research.

Availability of data and materials

The data sets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 23 November 2023 Accepted: 6 February 2024

Published online: 22 February 2024

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