



Taking light pollution effects on biodiversity into account in conservation measures : challenges and prospects. Case study of European bat species

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Taking light pollution effects on biodiversity into account in conservation measures: challenges and prospects

Case study of European bat species

Par Léa Mariton

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Dirigée par Dr Christian Kerbiriou, Dr Isabelle Le Viol, et Dr Brigitte Zanda
(HDR)

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“Si j’en avais le pouvoir, j’émettrais aujourd’hui un trou noir. Quelque chose comme un cône d’extinction forant au ventre l’épaisseur du jour. Pour rouvrir l’espace. Ce qui me terrifie, ce n’est pas ce chaos de clartés qui brouille la ville comme une avalanche de soleils. C’est qu’il n’y ait plus nulle part une seule ombre. Tout est féroce ment surexposé.”

– Alain Damasio, *So phare away*



Drawing: Antoine Mariton



Abstract

Electric lights have proliferated rapidly over the last century and have changed the night-time environment globally. Over the past decades, scientific studies have shown the effects of artificial light at night (ALAN) on biodiversity. Light pollution has been shown to disrupt a wide range of ecological processes and taxa. In this PhD, we aimed to fill some of the knowledge gaps that could prevent the effects of light pollution on biodiversity from being effectively addressed by mitigation measures. We used bats as model species because they are considered good indicators of the effect of anthropogenic pressures on biodiversity and because, being nocturnal, they are directly exposed to ALAN.

We advocated considering the temporal distribution of species in conservation measures, a prerequisite being to have access to knowledge on their temporal ecology. We used data from a national bat monitoring program (Vigie-Chiro) based on acoustic monitoring to characterise bat diel activity patterns (9807 nights monitored, 20 species). We found that bat species could be separated into three functional groups characterised by a crepuscular activity, an activity that occurs when it is completely dark or an intermediate activity. We showed variations of diel activity patterns depending on the season. Accounting for these complex diel activity patterns would help to design efficient mitigation measures. For instance, it would allow the design of part-night lighting schemes covering the range of activity of the target species.

Early emerging bats are mostly “light tolerant” species known to feed on insects attracted to lights. However, at the landscape scale, these species tend to be less abundant because of ALAN. This could be explained by disruptions in the diel activity patterns of bats due to ALAN, with potential consequences for population dynamics. Using the Vigie-Chiro dataset, we tested whether ALAN was responsible for such disruptions on a “light tolerant” species (*Eptesicus serotinus*). ALAN, and to a lesser extent moonlight, reduced its abundance. ALAN delayed activity, this delay was amplified during overcast nights, probably because cloud cover amplified skyglow. Further analyses suggested that two other “light tolerant” species might delay their activity because of ALAN. Thus, even “light tolerant” species should be protected from light pollution.

Where it is not possible to switch off lights, other mitigation measures include changing the intensity, directionality and spectrum of light. Many countries are retrofitting lighting equipment with light emitting diodes (LEDs). Despite potential impacts on biodiversity, few studies have focused on this shift. By reanalysing the data from a previously published study, we found that changes in light spectrum and intensity during such a shift have additive and interactive effects on bats. Bat activity decreased with increasing LED intensity. Using the Vigie-Chiro dataset, we showed that the adoption of LEDs would decrease landscape connectivity for bats, with this impact possibly being mitigated by better orienting the light flux. We recommended using LEDs with warmer colours and reduced light intensity.

Multiscale spatiotemporal approaches are needed to assess ALAN effect on biodiversity. Although some knowledge gaps remain, there is overwhelming evidence of the impact of light pollution on ecosystems. Mitigation measures are being developed, so there is a need to assess their effectiveness and possible improvements. Considering the reduction of ALAN at the landscape scale is a necessary next step, hence the emergence of the concept of dark ecological networks. A transdisciplinary project on lighting practices and their evolution in municipalities was initiated during this PhD. Indeed, as ALAN has not only ecological but also health and socio-cultural implications, a transdisciplinary perspective is needed to shift the paradigm from conventional lighting to new forms of lighting.

Résumé

Ce dernier siècle, les lumières électriques ont proliféré, modifiant l'environnement nocturne. Des études scientifiques alertent sur les effets négatifs de la lumière artificielle nocturne (LAN) qui perturbe de nombreux processus écologiques et taxons. Notre objectif a ainsi été de combler des manques de connaissances afin d'aider à une meilleure considération des effets de la pollution lumineuse sur la biodiversité dans les mesures de conservation. Nous avons utilisé les chiroptères comme modèles biologiques car ce sont de bons bioindicateurs de l'effet des pressions anthropiques sur la biodiversité et, étant nocturnes, ils sont directement exposés à la LAN.

Nous avons préconisé de considérer la distribution temporelle des espèces dans les mesures de conservation, un prérequis étant de connaître leur écologie temporelle. Nous avons utilisé les données d'un programme national de suivis acoustiques des chiroptères (Vigie-Chiro) pour étudier leur rythme d'activité nocturne (9807 nuits, 20 espèces). Nous avons montré que les espèces pouvaient être séparées en trois groupes ayant une activité crépusculaire, en cœur de nuit ou intermédiaire, avec des variations des rythmes d'activité selon les saisons. La prise en compte de ces rythmes complexes aiderait à concevoir des mesures de conservation efficaces, par exemple, en définissant des extinctions partielles de la LAN adaptées à des espèces cibles.

La plupart des chiroptères émergeant tôt sont des espèces « tolérantes à la lumière » pouvant se nourrir sous les lampadaires. Cependant, à l'échelle du paysage, ces espèces semblent moins abondantes à cause de la LAN. Cela pourrait s'expliquer par des perturbations de leur rythme d'activité influant possiblement les dynamiques de population. A l'aide des données Vigie-Chiro, nous avons testé si la LAN induisait de telles perturbations pour une de ces espèces (*Eptesicus serotinus*). La LAN, et dans une moindre mesure la lumière de la lune, réduisaient son abondance. La LAN retardait son activité, ce décalage était amplifié par la couverture nuageuse, possiblement à cause de son effet amplificateur du halo lumineux. Des analyses complémentaires ont suggéré que la LAN retardait l'activité de deux autres espèces « tolérantes à la lumière ». Ainsi, même ces espèces devraient être protégées de la LAN.

Lorsqu'éclairer est nécessaire, changer l'intensité, la direction ou le spectre des éclairages sont des mesures de réduction possibles. Nous assistons à une modernisation des éclairages avec des diodes électroluminescentes (LEDs). Malgré des impacts potentiels sur la biodiversité, peu d'études se sont intéressées à cette évolution. En réanalysant les données d'une étude publiée, nous avons montré que les changements de spectre et d'intensité accompagnant cette évolution avaient des effets additifs et interactifs sur les chiroptères. Quand l'intensité des LEDs augmentait, leur activité décroissait. Avec les données Vigie-Chiro, nous avons montré que les LEDs pouvait réduire la connectivité du paysage pour les chiroptères, cet impact étant atténué en orientant mieux les lumières. Nous avons recommandé d'utiliser des LEDs avec des couleurs plus chaudes et de moindre intensité.

Evaluer l'effet de la LAN sur la biodiversité implique des approches spatio-temporelles multi-échelles. Malgré les manques, il y a désormais suffisamment de preuves de l'impact de la LAN sur les écosystèmes. Les mesures de réduction étant en développement, évaluer leur efficacité et les améliorations possibles est indispensable. Penser la réduction de la LAN à l'échelle du paysage est une évolution impérative, d'où l'émergence du concept de trame noire. Un projet transdisciplinaire sur les pratiques communales d'éclairage et leurs évolutions a été initié pendant cette thèse. En effet, puisque la LAN n'a pas que des implications écologiques, mais aussi sanitaires et socio-culturelles, une perspective transdisciplinaire est indispensable pour changer nos façons d'éclairer.

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General introduction

“He saw the reflected glare of the lights of the city at what must have been around ten o’clock at night. They were only perceptible at first as the light is in the sky before the moon rises. Then they were steady to see across the ocean [...]”

Ernest Hemingway, The Old Man and the Sea

1. Light as major cue for biodiversity

Because of the Earth’s rotation about its axis, time is partitioned into regular cycles of day and night of about 24 hours. The overall fluctuations in the intensity of incident light (from the sun, moon, stars) between night and day are about six to eight orders of magnitude (in lux, see definitions **Box 1**) (Gaston et al., 2017). While the annual amount of light received at all places on Earth is roughly the same, the Earth’s orbit around the Sun is responsible for variations in the amount of daylight, darkness and semi-darkness over the year (Bennie et al., 2014b; Erkert, 1982; Gaston et al., 2017; Mills, 2008). Near the equator, there is almost no annual change in day length, whereas annual variations in day length become more pronounced at increasing latitudes (Bradshaw and Holzapfel, 2010a; Mills, 2008). Besides, visible light at night on Earth has also been shown to vary by about three orders of magnitude over the course of a month due to the lunar cycle (Kyba et al., 2017b). As these natural cycles of light and darkness have remained constant for extremely long geological periods, they have provided a rather invariant context structuring the environment of the majority of the eukaryotes (Bennie et al., 2014b). Species have therefore developed physiological, morphological and behavioural adaptations in response to these strong and predictable environmental fluctuations, with light becoming the most important cue for biological timings (Bennie et al., 2014b; Gaston et al., 2017).

1.1. The most important cue for biological timings

Early in evolution, in response to the 24-hour periodicity of their environment, most organisms (i.e. all eukaryotic and some prokaryotic organisms) developed circadian rhythms generated by a self-sustained endogenous pacemaker and entertained by external environmental

cues, with natural day-night cycles being one of the most important of these cues (Aschoff, 1989; Erkert, 1982; Guido et al., 2002; Hölker et al., 2010b) (**Figure 1**). Examples of circadian rhythms include endocrine oscillations in various hormones (e.g. melatonin and cortisol), rhythms of physiological parameters (e.g. body temperature) and behavioural patterns (e.g. activity-rest and sleep-wake cycles) (Guido et al., 2002). Circadian clocks thus play a key role in metabolism, growth and behaviour (Hölker et al., 2010b) and allow organisms to occupy a given temporal niche and coordinate their activity with that of other organisms with which they interact (e.g. conspecifics, predators, prey) (Aschoff, 1989; Erkert, 1982). Light is therefore a primary determinant of the species' temporal niche (Mills, 2008). Together with other factors such as temperature, competition and predation, it determines the position of species along a continuum ranging from strictly diurnal to strictly nocturnal species, with, for instance, species that are crepuscular (active during twilight), cathemeral (active both during day and night) or species whose strategy varies according to season and latitude (Bennie et al., 2014b; Mills, 2008). Nowadays, it is estimated that a substantial proportion of the global biodiversity is nocturnal (30 % of all vertebrates and over 60 % of all invertebrates) (Hölker et al., 2010b).

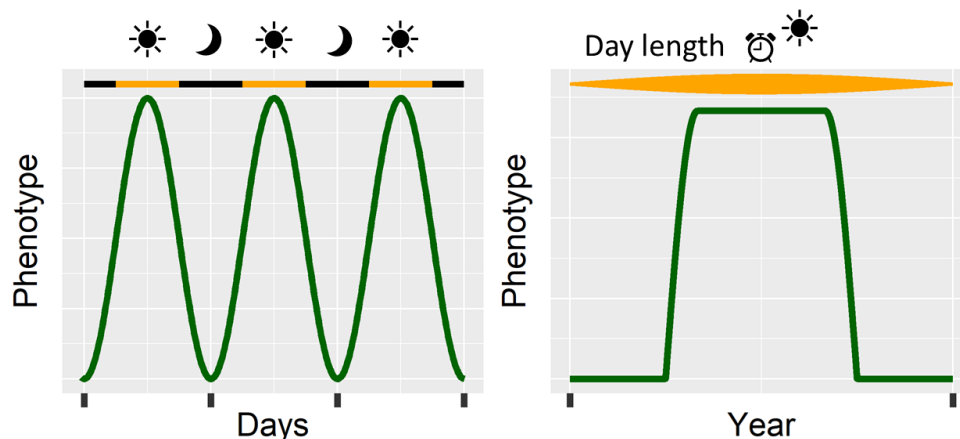


Figure 1: Daily circadian clock (left) and seasonal photoperiodic timer (right). The circadian clock cycles on a day-to-day basis. The photoperiodic timer can be seen as a “go/no-go physiological switch” that, once flipped, results in cascading events leading to season-specific physiology and behaviours.

Inspired from: Bradshaw and Holzapfel, 2010b

At a wider temporal scale, light has been shown to be a preeminent cue for determining species fitness in seasonal environments (Bradshaw and Holzapfel, 2010a). Indeed, to optimise their survival and reproductive success, living organisms must synchronise their phenology to exploit favourable seasons (e.g. for growth or reproduction) while mitigating the negative consequences of unfavourable seasons (e.g. through dormancy, diapause or migration)

(Bradshaw and Holzapfel, 2007; Helm et al., 2013). Organisms not only need to detect the optimal time to engage in season-specific behaviours, but also to be able to forecast the change of season to prepare for it (e.g. storing fat for dormancy or moulting before migration). Besides an internal circannual clock, many species thus use day or night length as an anticipatory cue to time seasonal events and regulate their behaviour and physiology accordingly, this is called photoperiodism (Bradshaw and Holzapfel, 2010a, 2007). In particular, such a mechanism has been shown to be a central component of fitness in temperate and polar seasonal environments (Bradshaw and Holzapfel, 2007).

Although less studied than annual and daily cycles (Kronfeld-Schor et al., 2013), lunar cycles, by inducing several environmental cycles (e.g. regular variations in illumination levels, tides), can also influence biological timings (Gaston et al., 2017). In particular, it has been shown that moonlight can affect reproduction and migration timings in terrestrial and marine ecosystems (Kronfeld-Schor et al., 2013). For instance, moonlight has been shown to drive mass vertical migration of zooplankton during Arctic winter (Last et al., 2016), to be an important external stimulus for mass spawning synchrony in corals (Kanievska et al., 2015) and to entertained a semilunar rhythm of zoea-release in the terrestrial crabs (Saigusa, 1980).

1.2. Implication of light in other key functions

Light not only plays a key role in biological timings, but also in a wide range of other functions affecting the fitness of organisms. Firstly, it should not be forgotten that light is a resource (Gaston et al., 2013). Indeed, sunlight, through photosynthesis, is converted into chemical energy by autotroph organisms and is therefore considered to be the ultimate source of energy that maintains the biosphere (Barber and Andersson, 1992).

Secondly, light is also an essential source of information for many organisms. For instance, to orientate themselves (e.g. during diel activity or migration), many species rely on bright celestial cues such as the sun, moon, stars and skylight polarization patterns (e.g. Able, 1982; Dacke et al., 2004, 2003; Foster et al., 2021, 2018; Papi and Pardi, 1963). Light is also used by some species to identify conspecifics and communicate. The best known example is the use bioluminescent signals by fireflies and glow-worms during courtship to attract conspecifics (Longcore and Rich, 2004; Owens et al., 2018), another example is the use of iridescence by animals: when light interferes with nanostructured biological materials, it can

generate bright, directional colours which can be used as visual signals in animals (e.g. to identify conspecifics, to determine their sex and age, to mark a territory) (Doucet and Meadows, 2009; Kelley et al., 2019). Light can also be used as an interspecific signal, for instance to lure preys (e.g. in glow-worms, Meyer-Rochow, 2007).

In summary, natural light and dark cycles are responsible for behavioural, physiological and morphological adaptations in most species. It has been suggested that nocturnality is an important step in the evolution of vertebrates (Hölker et al., 2010b). However, it is now threatened by widespread use of artificial light at night (ALAN), which is changing light and dark cycles at an unprecedented rate and threatens to render organisms' adaptations to these cycles dysfunctional or even ineffective.

2. The irruption of artificial light at night

Humans have long sought ways to extend their activity into the night. In pre-industrial times, ALAN (e.g. streetlights, store fronts, lighted buildings, etc.) was generated by burning materials such as wood or oil (Longcore and Rich, 2004). With the advent of electricity, increased economic prosperity and growing urbanisation, electric lights proliferated rapidly over the last century and changed the night-time environment all over the Earth (Kyba et al., 2011; Longcore and Rich, 2004). ALAN is therefore responsible for a widespread pollution called “light pollution”, which has been defined as “*the alteration of night natural lighting levels caused by anthropogenic sources of light*” (Falchi et al., 2016). Light pollution results from the direct effects of ALAN on its surroundings and from the “skyglow” which is the artificial light scattered by atmospheric constituents and reflected back towards the Earth (Gaston et al., 2015; Kyba et al., 2017a). Thus, although light pollution is generally linked to urbanisation, it is a diffuse pollution that can spread hundreds of kilometres from its sources to pristine sites and biodiversity hotspots otherwise not impacted by other anthropogenic pressures (Falchi et al., 2016; Guetté et al., 2018). Light pollution is a particular anthropogenic pressure as it does not directly respond to a human “physical” need (unlike agriculture or fishing, for instance) and because the alteration of darkness stops as soon as lights are switched off (unlike chemical pollution, for instance).

In 2016, Falchi et al. estimated that 23 % of the world's land surfaces between 75 °N and 60 °S, 88 % of Europe and almost 50 % of the United States experienced nights disrupted by light pollution (**Figure 2**). They showed that 80 % of the world's population lived under light-polluted skies and that more than a third could no longer see the Milky Way. In Europe, these figures were even higher with 99 % of the population living under light-polluted skies, 60 % of whom could no longer see the Milky Way. ALAN is still expanding, indeed, it has been shown that between 2012 and 2016, the world's artificially lit outdoor areas increased by 2.2 % per year with a growth in total radiance (see definitions **Box 1**) of 1.8 % (Kyba et al., 2017a).

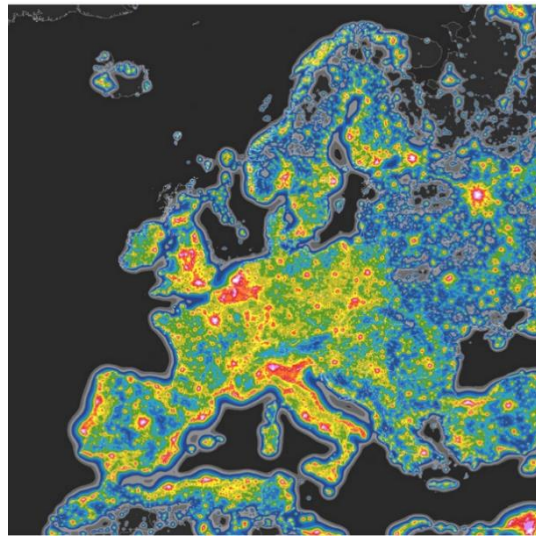


Figure 2: Maps of Europe's artificial sky brightness, in twofold increasing steps, as a ratio to the natural sky brightness (assumed to be $174 \mu\text{cd.m}^{-2}$) (see definitions **Box 1**).

Source: Falchi et al., 2016 (CC BY-NC 4.0)

Besides, ALAN is an energy and environmental issue, as it accounts for 16.5 % of the world's annual electricity production and 5 % of annual global greenhouse gas emissions (i.e. 1150 Mt of CO₂ per year) (Zissis et al., 2021). As a result, lighting policies have been implemented to increase energy efficiency and improve environmental performance. For instance, the European Design Directive established a framework for phasing out energy-intensive lighting equipment such as incandescent lamps and mercury vapor (MV) lamps in the European Union (Hölker et al., 2010a; The European Parliament and the Council of the European Union, 2009).

Prior to this directive, in 2005, the types of lamps conventionally used in the European Union were estimated to be sodium lamps (56 %: 9% low-pressure sodium (LPS) and 47%

General introduction

high-pressure sodium (HPS) lamps) and white lamps (43%: 32% MV lamps, 8% fluorescent lamps and 3% metal halide (MH) lamps) (Sánchez de Miguel et al., 2022; Van Tichelen et al., 2007). However, recent developments in lighting technologies, combined with the fact that lighting equipment is reaching the end of its life in developed countries, has resulted in a transition of the world's outdoor lighting stock from conventional lamp types to energy-efficient light-emitting diodes (LEDs) (Kerbiriou et al., 2020; Sánchez de Miguel et al., 2022). In 2017, the Spanish urban lighting park was already composed of about 56 % of LEDs, and by 2019, the British and French urban lighting parks were composed of about 51 % and 10 % of LEDs respectively (Sánchez de Miguel et al., 2022; Zissis et al., 2021).

While LEDs have been promoted to reduce energy consumption and economic costs, these goals can be undermined by a “rebound effect” in which higher luminous efficacy (see definitions **Box 1**) results in greater light use (e.g. greater spatial extent and higher illuminance) rather than energy and cost savings (Kyba et al., 2017a).

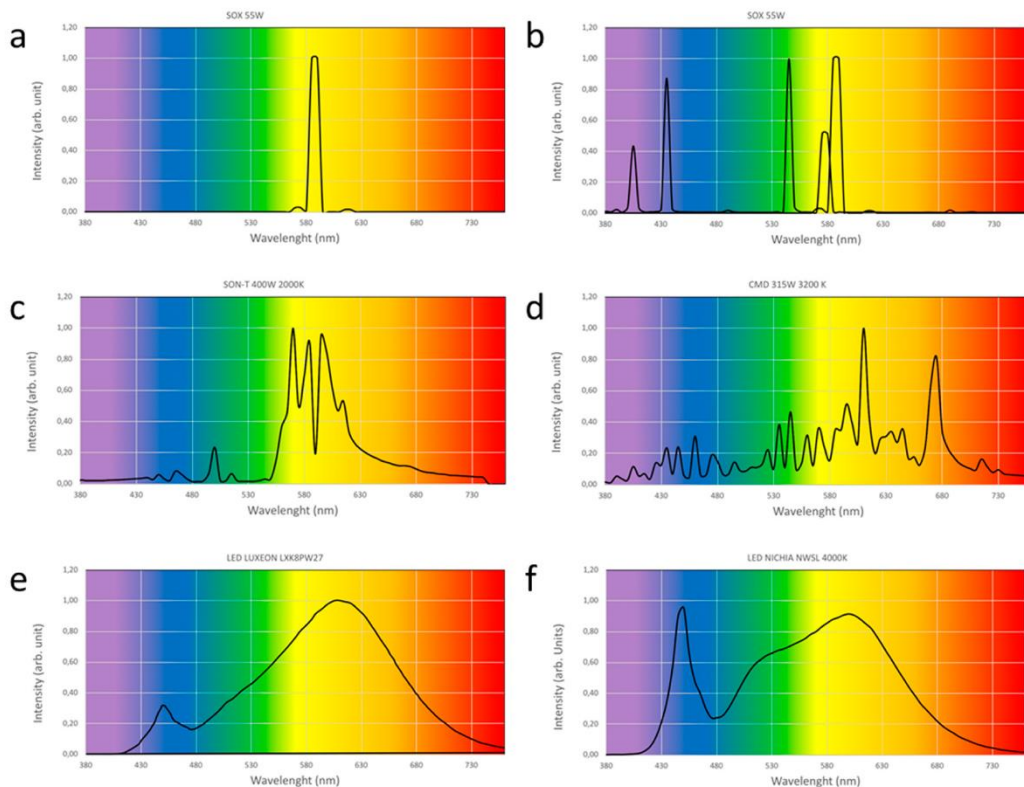
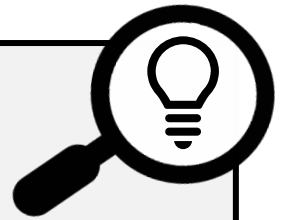


Figure 3: Spectra (visible domain 360-780 nm) of some conventionally lamp types used for outdoor lighting. Luminous intensities are normalized to the maximum value: (a) LPS lamp; (b) MV lamps; (c) HPS lamps; (d) ceramic MH lamps; (e) warm white LED (2700 K); (f) cool white LED (4000 K). Spectral data were measured by LAPLACE laboratory.

Source: Kerbiriou et al., 2020 (CC BY 4.0)



Box 1: Lighting terminology

Sources: (Choudhury, 2014; Stone, 2013)

A. Photometric measures (science of measurement of light in units that are weighted to reflect the sensitivity of the human eye)

Illuminance (E): measure of the amount of luminous flux incident on a surface per unit area. In the international system (SI) of units, it is measured in lux (lx), which is equal to one lumen per square meters (lm.m^{-2}).

Luminance (L): measure of the luminous intensity per unit area of light travelling in a given direction. It reflects how bright a surface appears to the human eye when we view it from a given direction. In SI units, it is measured in candelas per square meters (cd.m^{-2}).

Luminous efficacy (K): measure of how well a light produces visible light. In SI units, it is measured in lumens per watt (lm.W^{-1}).

Luminous intensity (I): measure of the wavelength-weighted power emitted by a light source in a particular direction per unit solid angle, based on the sensitivity of the human light. In SI units, it is measured in candelas (cd).

Luminous flux (Φ): measure of the perceived power of light adjusted to reflect the sensitivity of the human eye. In SI units, it is measured in lumen (lm).

B. Radiometric equivalents (science of measurement of light in any portion of the electromagnetic spectrum)

Radiometric	SI unit	Photometric	SI unit
Irradiance	W.m^{-2}	Illuminance	lx
Radiance	$\text{W.m}^{-2}.\text{sr}^{-1}$	Luminance	cd.m^{-2}
Radiant intensity	W.sr^{-1}	Luminous intensity	cd
Radiant flux	W	Luminous flux	lm

C. Other definitions

Correlated colour temperature (CCT): measure of the colour appearance of the light emitted by a light source. It is the temperature (in kelvins, K) of a black-body radiator that radiates light of comparable hue of the light source.

Electromagnetic spectrum: refers to the distribution of electromagnetic radiation according to their frequency or wavelength.

Wavelength: the distance between two corresponding points of a given wave. Wavelengths of light are measured in nanometres (nm).

Besides, the transition to LEDs had led to a change in the spectral composition (see definitions **Box 1**) of ALAN (Sánchez de Miguel et al., 2022). As a matter of fact, MV lamps, MH lamps and the LEDs used nowadays in outdoor lighting have a relatively broad spectrum with important emission peaks in the blue range (**Figure 3**). Conversely, LPS lamps emit narrow-band spectrum with a single energy peak in the yellow range and HPS lamps emit light over a wider range of wavelengths – including some blue and green light – but with an important emission peak in the yellow-orange range (Kerbiriou et al., 2020; Sánchez de Miguel et al., 2022). Thus, Sánchez de Miguel et al. (2022) showed, before and after 2013, a regionally widespread shift in the spectral composition of light emissions from a spectral composition associated mainly with HPS lamps to a spectral composition associated with white LEDs, with increased emissions in the blue part of the visible spectrum.

In the 1970s, astronomers were the first to warn against light pollution, as it hindered the detection of celestial objects and affected astronomical programs (Hölker et al., 2010a; Riegel, 1973). Since then, multiple other negative impacts of light pollution have been documented. While ALAN effects on human well-being and health have been recognised, a wide range of scientific papers have also highlighted the impacts of light pollution on biodiversity (Hölker et al., 2010a).

3. Ecological consequences of light pollution

In recent decades, scientists have warned of the adverse effects of light pollution on biodiversity (Longcore and Rich, 2004). At the individual and species level, ALAN has temporal and spatial implications. Indeed, by masking daily, monthly and annual light and dark cycles, light pollution disrupts biological timings. By triggering orientation/disorientation and attraction/repulsion behaviours, it affects the movements and spatial distribution of species. ALAN affects intra- and inter-species interactions by modifying competition and predation for instance. Ultimately, light pollution could have dramatic cascading consequences on population dynamics and ecosystem functions.

3.1. Disruptions of biological timings

As natural light is a major cue for biological timing, alterations in light and dark cycles have many consequences on biodiversity.

3.1.1. Disruptions of diel rhythms

Disruptions of circadian rhythms

By disrupting the natural daily cycle of light and dark, light pollution affects the circadian rhythm and physiology of species. Laboratory studies have shown that ALAN, even at dim levels, can disrupt circadian rhythms in a wide range of species (e.g. by disrupting the expression of clock genes, altering the production of hormones such as melatonin or corticosterone), with downstream consequences on health (e.g. reduced immunity, sleep loss, abnormal weight gain, alteration of reproductive, cognitive and metabolic functions) (Bedrosian et al., 2011; Bumgarner and Nelson, 2021; Dominoni et al., 2016; Durrant et al., 2015; Evans et al., 2007; Fonken et al., 2013, 2010; Kupprat et al., 2020; West et al., 2011). The intensity and existence of these disruptions have been shown to vary with light spectrum (e.g. the photopigment responsible for the decrease or suppression of melatonin production has a maximum spectral sensitivity at blue wavelengths) and light intensity (however, even very low light levels could have an impact) (e.g. Aubé et al., 2013; Dominoni et al., 2022; Evans et al., 2007; Kernbach et al., 2020). While much attention has been paid to the mechanisms explaining ALAN impacts on the health of humans and model species, less is known on ALAN effect on the health of wild populations (Dominoni et al., 2016). Indeed, only a few studies, mainly conducted in laboratory, show how circadian, and more generally physiological, disruptions due to ALAN could lead to health impacts and lower survival on wild species (Chen et al., 2021; Dominoni et al., 2022; Kernbach et al., 2020; Touzot et al., 2021). Such studies raise the need to assess the long-term effect of these disturbances on individual fitness and population dynamics as well as to explore potential cascading effects to large ecological and epidemiological scales.

Disruption of diel biological rhythms

A growing body of literature documents ALAN impacts on the timing of diel biological events and rhythms in wildlife. In diurnal and crepuscular species, light pollution can disrupt

sleep at night (e.g. Aulsebrook et al., 2020; Kolbe et al., 2021; van Hasselt et al., 2021; Wang et al., 2021) and/or induce or increase activity into the night (e.g. Alaasam et al., 2021; Amichai and Kronfeld-Schor, 2019; Dominoni et al., 2022; Parlin et al., 2022; Secondi et al., 2021; Taylor et al., 2022). A well-known example of these ALAN-induced disturbances is the earlier initiation of dawn chorus and night-time singing in birds, with cascading consequences for breeding success (Kempenaers et al., 2010; Longcore and Rich, 2004; Miller, 2006) (**Figure 4**). Conversely, ALAN has been shown to alter and curtail the activity of nocturnal species (e.g. Duarte et al., 2019; Le Tallec et al., 2013; Lynn et al., 2021; Rotics et al., 2011).

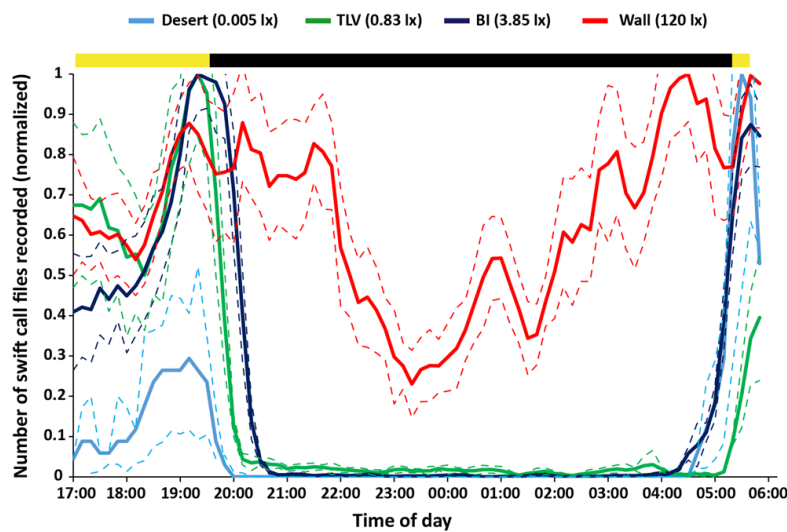


Figure 4: Effects of ALAN on the diel activity patterns of Common swifts (*Apus apus*). Multi-night mean of the number of acoustic recording containing swift calls per 10-min bins. The bar at the top depicts day/night (sunrise/sunset) cycle (yellow = day, black = night). At the three low-ALAN sites (Desert, TLV, BI) swift activity ended around sunset, while at the high-ALAN site (Wall) activity continued throughout the night.
Source: Amichai and Kronfeld-Schor, 2019 (CC BY 4.0)

For instance, some localised studies have shown that roost illumination can delay or even stop the emergence of some bat species (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021; Straka et al., 2020). Two other localised studies suggested that bat activity may also be delayed at foraging and commuting sites because of ALAN (Haddock et al., 2019a; Stone et al., 2009). This could result in a reduced time-budget for bats to forage and a desynchronisation with the peak of activity of their prey. Ultimately, this could alter individual fitness and possibly population dynamics.

It is therefore of utmost importance to pay more attention to the impacts of ALAN on the diel activity pattern of nocturnal species such as bats. For instance, it would be necessary to assess the range of species affected (e.g. do they share similar functional traits? could the alteration of the diel activity pattern of one species have consequences on the diel activity pattern of other species in the same trophic chain?, etc.), the scale at which such impacts may be observed (e.g. are they only local disruptions in particular contexts or could they be observed at larger scales?) and to assess light parameters that may drive such disturbances (e.g. are low levels of light, similar to moonlight, likely to trigger alterations in the diel activity pattern of nocturnal species? does the magnitude of the alterations depend on the spectrum of emission?, etc.).

3.1.2. Disruptions of annual rhythms

Light pollution masks primordial luminous cues for biodiversity, such as the length of day and night, which allow species to adapt their physiology and behaviours to a seasonal environment (Gaston et al., 2017). Among the seasonal behaviours that have been shown to be disrupted by ALAN are reproduction behaviours of a wide range of taxa. For instance, for birds, dawn and dusk singing have been shown to develop earlier in the year in light-polluted sites (**Figure 5**, Da Silva et al., 2015) and that lay date tended to be earlier due to ALAN (de Jong et al., 2015; Senzaki et al., 2020); for mosquitoes, ALAN can cause females to avert overwintering diapause and become reproductively active (Fyie et al., 2021); for captive nocturnal primates, the first seasonal oestrus was earlier in females exposed to ALAN compared to females exposed to moonlight (Le Tallec et al., 2015); for deciduous woody plants, ALAN advanced the date of budburst and the magnitude of this phenological change was correlated with ALAN intensity (ffrench-Constant et al., 2016; Meng et al., 2022). Other seasonal behaviours disrupted by light pollution include bird migration (Smith et al., 2020), insect diapause (Mukai et al., 2021), the colouring of leaves of deciduous woody plants (Meng et al., 2022).

Overall, the consequences of these phenological perturbations on fitness are mostly unknown, but they might result in dramatic potential phenological mismatches (e.g. between species in the same trophic chain or between species and their abiotic environment). Indeed, as noted in the first part of this introduction, photoperiodism has been shown to be a central component of fitness in temperate seasonal environments (Bradshaw and Holzapfel, 2007), and

the consequences of the ALAN-induced alterations of this key mechanism for biodiversity should therefore be the focus of future studies.

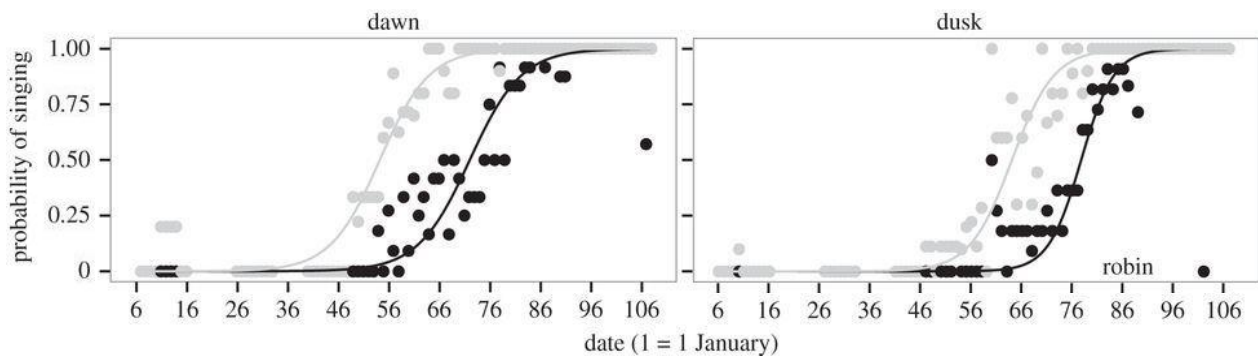


Figure 5: Probability of singing at dawn and dusk according to the day of the year for European robin (*Erithacus rubecula*) at dark and lighted sites. The points and lines represent the observed and the predicted daily probability of singing at dawn (left panel) and dusk (right panel) respectively. Sites with ALAN are in grey and dark sites in black. Robins are more likely to sing at dawn and dusk earlier in the season at lighted sites.

Source: Da Silva et al., 2015 (CC BY 4.0)

3.1.3. Disruptions of monthly rhythms

As light pollution can mask natural lunar cycles, it is likely to disrupt biological events triggered by them (e.g. reproduction, migration). For instance, corals synchronise their spawning using, among other external cues, moonlight. When exposed to light conditions similar to those created by ALAN, this synchrony has been shown to be disrupted (Ayalon et al., 2020; Kaniewska et al., 2015). However, to date, these studies are among the very few papers documenting the impacts of ALAN on monthly rhythms related to lunar cycles (Gaston et al., 2017).

Interestingly, moonlight can also influence the foraging behaviours of nocturnal species. It can increase the efficacy of visually hunting predators and, consequently, induce a moonlight avoidance strategy for their prey (known as “lunar phobia”) (Kronfeld-Schor et al., 2013; Saldaña-Vázquez and Munguía-Rosas, 2013). For instance, it has been suggested that moonlight had a negative effect on the spatiotemporal distribution of bats (Appel et al., 2017; Gomes et al., 2020; Kolkert et al., 2020). However, this effect of moonlight on bats has not been much studied in temperate regions and is still discussed (Saldaña-Vázquez and Munguía-Rosas, 2013).

Determining whether moonlight can indeed negatively affect the behaviours of nocturnal species such as bats would help predict the potential effect of light pollution on them. Indeed, during a full moon under clear conditions, ambient light levels have been estimated to be around 0.1 - 0.3 lux while, in the urban skyglow, ambient light levels have been estimated to be around 0.15 lux (Gaston et al., 2013). Thus, the skyglow might trigger similar responses to those triggered by the full moon, but unlike moonlight, its pressure on nocturnal species is constant. It would therefore be interesting to assess how low but constant light levels, similar to moonlight, may affect nocturnal species and to assess the nature of the interaction between moonlight and ALAN intensity for biodiversity (e.g. do they trigger additive or interactive effects? does lunar phobic species still respond to variations of moonlight intensity in light polluted-contexts? etc.).

3.2. Disruptions of spatial distribution and movements

In addition to disrupting the temporal distribution of species, light pollution has been shown to modify their spatial one.

3.2.1. *Attraction and repulsion*

Light pollution have been known for long to alter the distribution of mobile species, by attracting some and repelling others (Longcore and Rich, 2004). Many taxa are known to be positively phototactic (i.e. to be attracted by light sources) (e.g. nocturnally migrating birds: Poot et al., 2008; Van Doren et al., 2017; spiders: Davies et al., 2017; Parkinson et al., 2020; fish: Becker et al., 2013). Such attraction can have dramatic impacts on fitness. For instance, many insect species (e.g. Bolliger et al., 2022; Camacho et al., 2021; Kühne et al., 2021; Owens et al., 2019) aggregate in the vicinity of lights where they suffer increased mortality (through exhaustion, predation, injury), this phenomenon that has been called the “vacuum cleaner effect” (Camacho et al., 2021; Eisenbeis, 2006). These aggregations then attract species feeding on insects, such as nocturnal birds (Rodríguez et al., 2020) or insectivorous bats (Rydell, 1992). In particular, edge- and open-space-foraging bat species (mainly mid- and long-range-echolocators whose flight is usually considered to be “fast”, e.g. *Nyctalus* spp., *Pipistrellus* spp.) are known to forage under streetlights, hence exploiting this predictable insect biomass

(Azam et al., 2018; Rydell, 1992; Salinas-Ramos et al., 2021; Stone et al., 2015a; Zeale et al., 2018). These bat species are therefore usually considered to be “light tolerant” species. Overall, the effect of attraction on fitness can be highly variable according to the species, including causing increased mortality for some, but also creating foraging opportunities and new competition interactions for others.

Conversely, other taxa have been shown to be negatively phototactic (i.e. to experience repulsion at the vicinity of light sources), probably due to higher predation risks (e.g. mammals: Bird et al., 2004; Farnworth et al., 2016; crustaceans: Czarnecka et al., 2022); insects: Farnworth et al., 2018; birds: Syposz et al., 2021, fish and zooplankton: Geoffroy et al., 2021). For instance, narrow-space-foraging bat species (mainly short-range-echolocators whose flight is usually considered to be “slow”, e.g. *Myotis* spp., *Plecotus* spp.) avoid light at all spatial scales, they are thus usually considered as “light intolerant” species (Lacoeuilhe et al., 2014; Rydell, 1992; Salinas-Ramos et al., 2021; Spoelstra et al., 2017; Voigt et al., 2021; Zeale et al., 2018). Indeed, despite foraging opportunities at the vicinity of light sources, these species have a low and slow flight that may result in a reduced ability to avoid predation compared to open- and edge-space-foraging species (Rydell, 1992; Rydell et al., 1996). As the aggregation of insects near light sources might deplete dark areas from insects, these species might suffer from a reduced availability of foraging resources with potential consequences on their fitness. It should also be noted that species that might be attracted to light sources when foraging (due to the greater availability of prey at their vicinity) may experiment repulsive behaviours in other contexts. For instance, even the commuting behaviour and movements of “light tolerant” bat species are affected by light pollution (e.g. lower probability of crossing gaps in tree cover with increasing light levels (Hale et al., 2015), increased flight speed near ALAN (Barré et al., 2020; Polak et al., 2011)).

Eventually, at the landscape scale, due to its attraction/repulsion effects, light pollution can create a “barrier effect” leading to a reduction in functional connectivity for species avoiding light sources, or trapped at their vicinity, and thus increase landscape fragmentation (Grubisic et al., 2018; Korpach et al., 2022; Laforge et al., 2019). Although more difficult to study than the local effect of light pollution on the behaviour of individuals, studies on this potential reduction in functional connectivity due to ALAN at the landscape scale are imperative. Indeed, connectivity is critical for the survival of populations at a time when habitat fragmentation has become a major factor in the decline of biodiversity (Fischer and

Lindenmayer, 2007). As advocated by Laforge et al. (2019), it would be useful to integrate conservation issues into urban planning by determining, for instance, where light points should be removed as a priority or which light parameters can be changed to restore some connectivity.

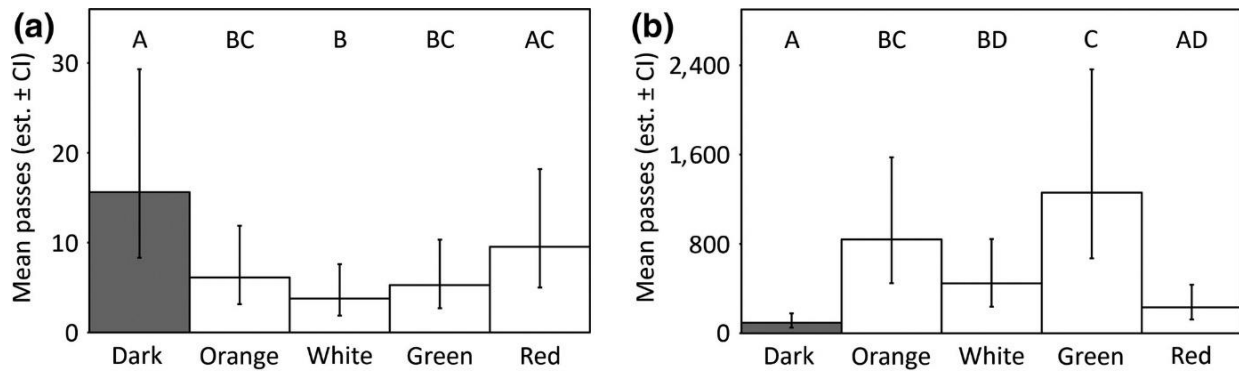


Figure 6: Overall bat activity around lights of with different emission spectra. Mean number of passes (a proxy for bat activity) made by (a) *Myotis* spp. and (b) *Pipistrellus* spp. on the lit side of hedgerows during dark control and light treatment nights. Letters identify treatments that differ significantly from each other. Red light had no effect on any species. *Myotis* spp. (slow, narrow-space-foraging species) avoided orange, white and green light, while *Pipistrellus* spp. (fast, edge-space-foraging species) were more active at these light types compared to dark controls. No effect of light was found for *Nyctalus* and *Eptesicus* spp.
Source: Zeale et al., 2018 (CC BY 4.0)

Finally, it should be noted that for some taxa, the magnitude (or even the existence) of the negative or positive phototaxis has been shown to vary according to the spectra of the light source (e.g. for birds: Aulsebrook et al., 2020; Poot et al., 2008; for crustaceans: Czarnecka et al., 2022). In particular, many studies showed that because of the ultraviolet (UV)-green-blue visual sensitivity of airborne and terrestrial invertebrates, light sources emitting a high proportion of short-wavelength light tend to have a stronger attractive effect on them (e.g. Bolliger et al., 2022; Lockett et al., 2021; Pawson and Bader, 2014; Somers-Yeates et al., 2013). Such increased attractivity can then affect higher trophic levels such as bats. For instance, *Pipistrellus* species (edge-space-foraging bat species usually considered to be “light tolerant”) have been shown to be more abundant around white and green lights compared to red ones (Spoelstra et al., 2017; Zeale et al., 2018) (**Figure 6**). Likewise, *Pipistrellus* species have been shown to be more abundant around MH and MV lamps compared to LPS lamps and LEDs, because MH and MV lamps emit UV and hence attract more insects (Lewanzik and Voigt, 2017; Stone et al., 2015b; Straka et al., 2019). On the reverse, *Myotis* and *Plecotus* species

(narrow-space-foraging bat species usually considered to be “light-intolerant”) have been shown to be less abundant around white and green lights compared to red ones (Spoelstra et al., 2017; Zeale et al., 2018) (**Figure 6**).

As specified in the second part of this introduction, the renewal of public lighting equipment in developed countries is leading to a change in the spectral composition of artificial light emissions, which is becoming “whiter” due to the large-scale adoption of LEDs that emit more in the blue part of the visible spectrum than the conventional sodium lamps (Kyba, 2018; Sánchez de Miguel et al., 2022). Overall, as the most commonly used LEDs currently have a broad spectrum of emissions, they are likely to trigger multiple behavioural (e.g. repulsion/attraction) or physiological responses in species (Sánchez de Miguel et al., 2022). It is therefore urgent to assess how this shift in lighting technology affects (or will affect) biodiversity.

3.2.2. Disorientation

A mechanism that has been proposed to explain the attraction and repulsion of species to light sources is the disruption of their orientation by light pollution (Boyes et al., 2020; Longcore and Rich, 2004). A common example in the scientific literature is how loggerhead (*Caretta caretta*) hatchlings fail to orient themselves toward the sea because of light pollution (Longcore and Rich, 2004; Salmon et al., 1995). However, a growing body of literature now documents disorientation in other taxa. For instance, by obscuring natural celestial cues, light pollution disrupts orientation behaviours in dung beetles (*Scarabaeus satyrus*, Foster et al., 2021), light sources impair visual cues essential for nocturnally migrating birds, thereby disorienting them (Van Doren et al., 2017), artificial skyglow disrupts the lunar compass of amphipods (Torres et al., 2020).

3.3. Disruption of communication

As some species rely on luminous cues to communicate, light pollution can alter interactions between individuals. The best known example is the disruption of mating behaviours and success of bioluminescent fireflies and glow-worms (Bird and Parker, 2014; Firebaugh and Haynes, 2016; Owens and Lewis, 2022). Besides, light pollution does not only

affect visual communication between individual, it can also disrupt sound communication. For instance, ALAN has been shown to directly affect the calling frequency of female moths (*Yponomeuta cagnagellus*, Cieraad et al., 2022) and to lead to an increase in calling effort in a wild frog (*Engystomops pustulosus*, Cronin et al., 2022)

3.4. Effects on communities and inter-species interactions

By inducing a wide range of disruptions at the individual and species levels, light pollution has been shown to have cascading impacts on community composition (e.g. invertebrates: Davies et al., 2017, 2012; Grubisic and van Grunsven, 2021; Kehoe et al., 2022; Khattar et al., 2022; Lockett et al., 2021, birds: (La Sorte and Horton, 2020; McNaughton et al., 2021) and interspecies interactions (Longcore and Rich, 2004).

3.4.1. Predation

Light pollution has been shown to alter predation patterns (Longcore and Rich, 2004). By eliciting or enhancing the activity of certain species at night and increasing the predation efficiency for visual predators, ALAN can create new predator-prey interactions and disrupt existing ones (e.g. insects-insects: Miller et al., 2017; fish-sessile invertebrates: Bolton et al., 2017; birds-insects: Negro et al., 2000). Furthermore, as some taxa suffer from a positive phototaxis, they aggregate near light sources and attract predators that are willing to exploit this predictable feeding biomass. For instance, owls (Rodríguez et al., 2020), “light tolerant” (i.e. edge- and open-space foraging) bat species (Rydell, 1992) and even diurnal species (Negro et al., 2000) have been shown to forage on invertebrates attracted to streetlights at night. It has also been shown that spiders were more abundant in illuminated sites where the number of prey items captured in their web is higher than in dark sites (Parkinson et al., 2020).

Light pollution can also disrupt defence strategies of prey. In particular, moths have been shown to reduce their anti-bat defensive behaviours under lit conditions, with ALAN reducing their ability to evade predation (Minnaar et al., 2015; Svensson and Rydell, 1998; Wakefield et al., 2015) (**Figure 7**). ALAN has also been found to decrease the efficacy of camouflage at night in intertidal littorinid snails (McMahon et al., 2022).

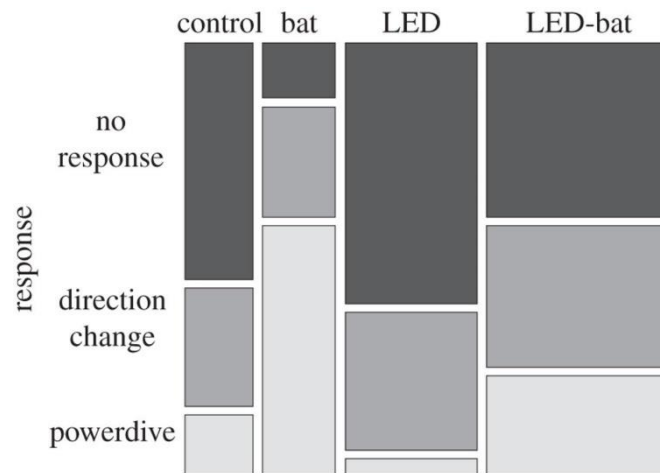


Figure 7: Proportion of moth flight responses to bat echolocation calls under LED-lit and unlit conditions. Columns are proportional to sample size. The number of powerdives (i.e. evasive flight behaviours) is significantly higher under the “LED-bat” treatment than under the “LED” treatment but lower than under the “bat” treatment. LED streetlights thus reduce the anti-predator behaviour of moths.

Source: Wakefield et al., 2015 (CC BY 4.0)

3.4.2. Competition

As light pollution can expand or restrict the availability of time and space for species activity, it can influence the degree of niche overlap between species and result in changes in competitive communities (Bennie et al., 2015; Longcore and Rich, 2004; Salinas-Ramos et al., 2021). For instance, Salinas-Ramos et al. (2021) shown that ALAN influences niche segregation between the two “light-tolerant” species *Pipistrellus pipistrellus* and *Pipistrellus kuhlii*. In particular, *P. pipistrellus* showed a less marked association with artificially illuminated sites when the occurrence of *P. kuhlii* was included in the modelling, suggesting potential competition for illuminated sites. More generally, ALAN may alter interspecific competition in favour of species that are able to benefit from the new set of conditions created by light pollution with indirect consequences for their competitors (Bennie et al., 2015).

3.4.3. Pollination and seed dispersal

A growing body of literature shows that light pollution disrupts nocturnal pollination networks and adversely affects the reproductive success of plants, with negative changes extending even to daytime pollinator communities (Giavi et al., 2021; Knop et al., 2017).

Similarly, by disrupting communities, ALAN can potentially alter seed dispersals. For instance, it has been shown that *Carollia sowelli* (a frugivorous bat species) harvested fruits more often at dark sites than at illuminated ones, with ALAN therefore having the potential to reduce the probability of successful seed dispersal by bats (Lewanzik and Voigt, 2014).

3.5. Light pollution impacts on population

The concept of niche has been shown to be a confusing and evolving idea in ecology (Devictor et al., 2010; McInerny and Etienne, 2012), however one definition that is still used in many studies is that conceptualised by Hutchinson (1957): the niche is an attribute of a species or population and is defined as an hyper-volume in the multidimensional space of biotic and abiotic variables within which a species could exist indefinitely. This raise the question of whether the new biotic and abiotic conditions resulting from the intrusion of ALAN into a landscape fit within the niche of a given species or whether ALAN is likely to threaten the persistence of populations of that species.

It should be noted that light pollution, although spreading far from its sources, remains strongly correlated with urbanisation. Disentangling its effects from those of other pressures such as impermeabilization, chemical pollution or noise pollution is therefore an important concern when assessing its impact on populations. Some studies have even pointed out that possible interactions between light and other anthropogenic pressures should be taken into account (e.g. noise pollution (Halfwerk and Jerem, 2021; Smit et al., 2022; Wilson et al., 2021), night warming due to urban heat islands (Miller et al., 2017)).

Thus, assessing the long-term effects of ALAN on populations remains a major research challenge. Browning et al. (2021) identified ALAN as a pressure that can reasonably be considered as a driver impacting bat populations, but there is a lack of studies directly linking light pollution to bat population trends. Likewise, light pollution has also been identified as a potential driver of global declines in insect populations (Owens et al., 2019), but few studies show direct evidence of ALAN effect scaling up to impact insect populations (Boyes et al., 2020) (however, see at local scale : Boyes et al., 2021; van Grunsven et al., 2020).

Overall, over the last decades, an explosion of scientific studies has been documenting the effects of light pollution on many ecological processes. While studies conducted at local scales or in laboratory allow to assess finely how ALAN is susceptible to alter species physiology and behaviours, studies conducted at wider scales are needed to assess its contribution to habitat fragmentation and loss and infer the long-term effect of light pollution on population dynamics (Azam et al., 2016; Gaston and Bennie, 2014).

However, a question remains: how does light pollution relate to other pressures? Are these impacts rather anecdotal or should they be the subject of urgent conservation measures? Given the magnitude and diversity of the impacts of ALAN presented in this third part of the introduction, it would seem that the second option should be favoured. This is the opinion presented by Owens et al., (2019) who stressed that light pollution, along with habitat loss, chemical pollution, invasive species and climate change, was contributing to the decline of insect populations worldwide. This also seems to emerge from the review of Browning et al. (2021), which placed light pollution as one of the six drivers of changes in European bat populations, alongside agricultural practices and the loss of forest areas. In comparison they considered that there was insufficient evidence to affirm that climate change and urbanisation were contributing to changes in European bat populations. Eventually, it should also be noted that, in 2021, the International Union for Conservation of Nature (IUCN) congress recognised the importance of the impacts of light pollution on biodiversity by adopting a motion advocating for “*taking action to reduce light pollution*” (IUCN World Conservation Congress, 2021).

4. Mitigating light pollution effects on biodiversity: knowledge gaps and plan of the thesis

Although ALAN is thus associated with multiple energy, financial and environmental issues, it is also a space planning tool associated with many social uses (e.g. security and safety of goods and people, enhancement of architectural heritage, marketing, etc.) (Challéat et al., 2021). The reduction of ALAN therefore involves compromises between the needs of humans for light and the needs of biodiversity for darkness. In particular, the five most commonly cited management options for reducing light pollution are: (i) preventing dark areas from being lit, (ii) limiting the duration of artificial lighting, (iii) reducing light trespass into areas that are not intended to be lit, (iv) reducing light intensity and (v) changing the spectral composition of

ALAN (Gaston et al., 2012). As lighting equipment reaches its end of life in developed countries, we are at an important crossroads in lighting management. Assessing the effectiveness of mitigating measures against light pollution is thus becoming a pressing challenge for scientists and managers.

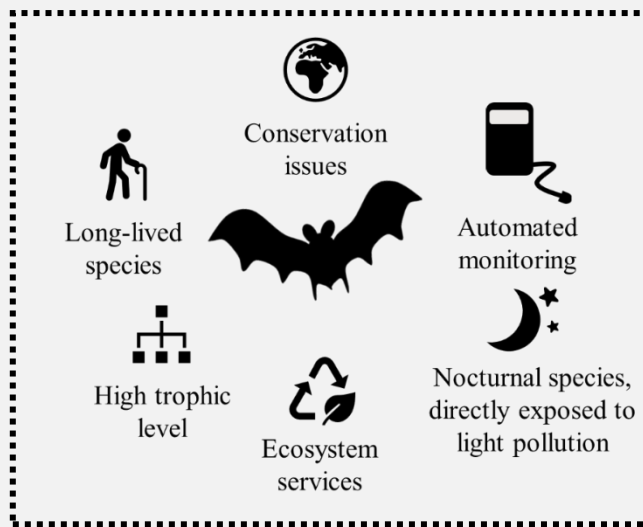
Limiting the duration of lighting is reflected in the field by the adoption of part-night lighting (PNL, i.e. switching off lighting in the middle of the night) schemes, aimed primarily at avoiding lighting when the human need for light is lowest. PNL schemes are increasingly being implemented across Europe (Bennie et al., 2014a). For instance, in France an increasing number of municipalities have switched off public lighting in the middle of the night during certain periods of the year (Lapostolle and Challéat, 2020) while the decree of 27 December 2018 on the prevention, reduction and the limitation of light pollution (*Arrêté du 27 décembre 2018*, 2018) sets out regulations on when parks, heritages, car parks or store fronts must switch off lights.

While PNL schemes can save energy and reduce lighting costs, they can also be valuable mitigation measures of the impacts of light pollution on biodiversity. To do this, light switch-off times should not only take into account key periods for human light needs, but also key periods for the dark needs of biodiversity. Therefore, knowledge of the diel activity patterns of species would be necessary to design and implement PNL schemes. Indeed, to date, PNL schemes have proven insufficiently effective in fully reducing the effects of ALAN on nocturnal species such as bats, precisely because they do not encompass their range of activity (Azam et al., 2015; Hooker et al., 2022).

In this context, Day et al. (2015) described the diel activity pattern of *Rhinolophus ferrumequinum* in south-west England and recommended switching off lights before midnight. However, this study covered only eight sites and one species. Other knowledge on diel activity patterns of bat species is scattered in the scientific and grey literature, in studies of limited taxonomic, spatial and temporal range. These studies could be synthesised in a review such as Jones and Rydell (1994) on the timing of bat emergence from roosts. However, it would not provide directly comparable data between species and would not cover the full environmental gradient that a species may encounter over its distribution range. In comparison, as advocated by Newson et al., 2015, the deployment of citizen science programs based on passive acoustic monitoring (PAM) offers great opportunities to monitor biodiversity at unprecedented

spatiotemporal scales and could therefore be an emerging opportunity to provide new insights in bat temporal ecology.

Box 2: Insectivorous bats as model species to study the impacts of light pollution on biodiversity



Using insectivorous bats as model species to study the impacts of light pollution on biodiversity

- ⇒ Bats are increasingly threatened worldwide and **all bats species are protected in Europe** (Azam et al., 2015; Mickleburgh et al., 2002).
- ⇒ Insectivorous bat species provide **ecosystems services**, in particular pest control (e.g. Ancillotto et al., 2022; Charbonnier et al., 2021).
- ⇒ **PAM and recent development of automated identification** of bat echolocation calls allow data to be collected on wide spatiotemporal scales.
- ⇒ As there are long-lived species and as they occupy high trophic levels, it has been suggested that **population trends of insectivorous bats may reflect those of lower trophic levels** (Jones et al., 2009). More generally, insectivorous bats have been suggested as **good bioindicators** of the response of biodiversity to anthropogenic pressures (Russo et al., 2021).

In the first chapter of this PhD, we thus intended to characterise the **diel activity patterns of bat species so that their consideration in mitigation measures** can help conservation. Indeed, bats are considered as good bioindicators of the responses of biodiversity to anthropogenic pressures (Jones et al., 2009; Russo et al., 2021) and, because they are nocturnal, they are directly exposed to light pollution (see **Box 2** for further information on the use of bats as model species).

We used data from the national citizen science program “Vigie-Chiro” (see **Box 3**) to design a method to describe the diel activity patterns of bats based on standardised and comparable metrics. By extracting times of key descriptors and describing bat activity distribution throughout the night, we intended to answer the following questions:

- (1) Can we distinguish functional groups of bat species to inspire multi-taxa approaches in conservation based on diel activity patterns?**
- (2) Should conservation measures take into account the variations in bat diel activity patterns according to the period of the year?**

We intended to illustrate how such new insights in bat diel activity rhythm **can be integrated in pre-existing conservation measures such as PNL**. This study is accepted *Biological Conservation* (under minor revisions):

- **Mariton, L., Le Viol, I., Bas, Y., Zanda, B., Kerbirou, C., 2022.** Characterising diel activity patterns to design conservation measures: case study of European bat species. (*accepted*)

It is also interesting to note that the bat species known to emerge early are mostly “light tolerant” species, which can feed on the aggregation of insects around light sources (Jones and Rydell, 1994; Rydell, 1992). Thus, implementing PNL schemes covering their peak of activity might seem a questionable measure at first sight.

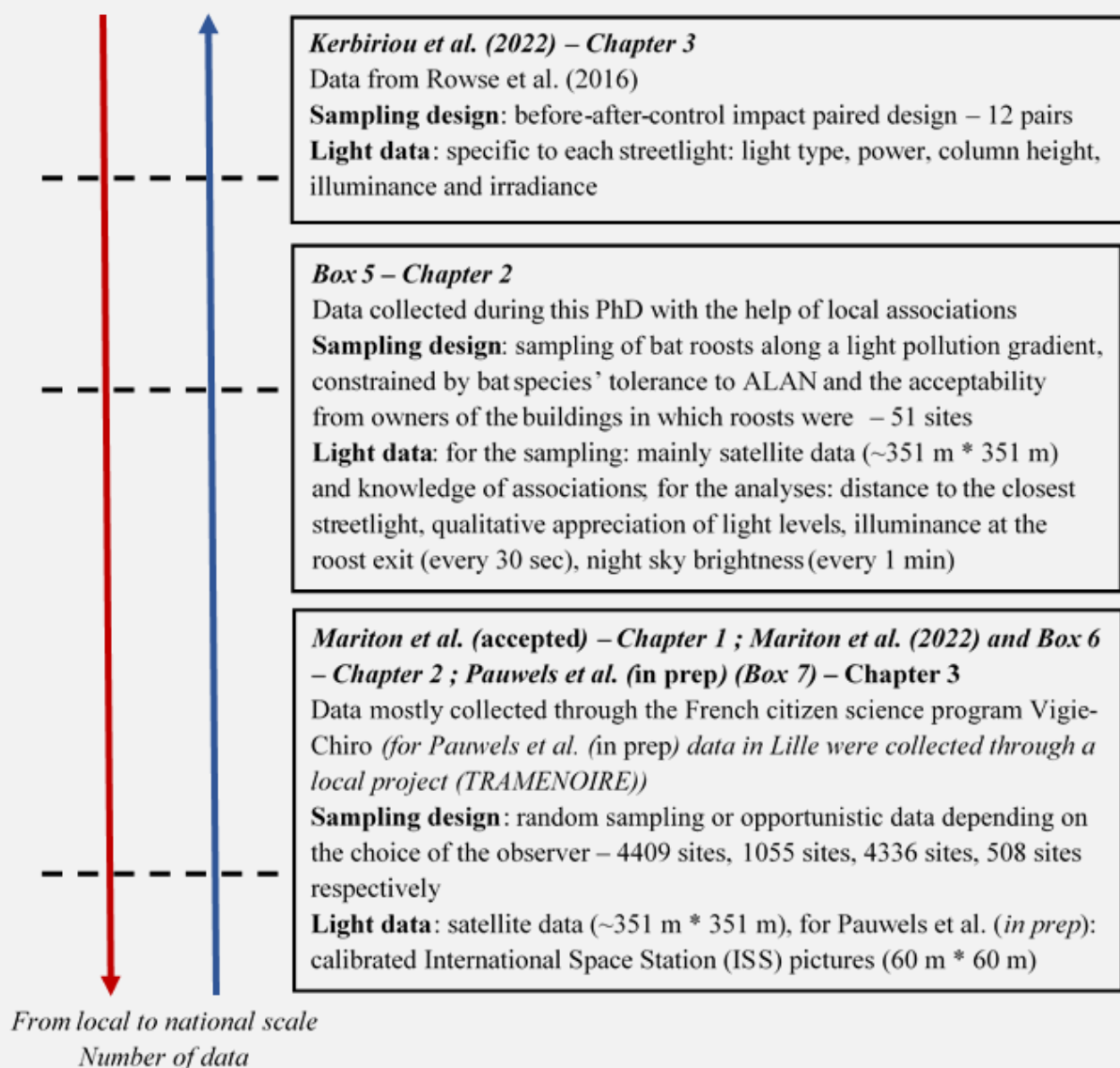
However, Azam et al., (2016) showed that while open- and edge-space-foraging bat species are considered to be “light tolerant” at local scale, at the landscape scale the activity of some of these species (*P. pipistrellus*, *P. kuhlii* and *Eptesicus serotinus*) was lower in light-polluted sites. Among the hypotheses that could explain such a different effect of ALAN on bats according on the spatial scale considered, there is the hypotheses that light pollution,



Box 3: Data acquisition

All biological data used in this PhD were collected in the field. Data on bat activity were collected using PAM devices, which therefore did not generate any disturbance. No artificial light was introduced or modified by us. We used several sources of data to conduct studies at different scales that could provide complementary information on the impact of light pollution on bats.

Control of the sampling design
Precision of the data describing ALAN



Biological and light data used in the different studies presented in this PhD

Box 3: Data acquisition

2



As shown in the figure above, most of the studies presented in this PhD were conducted thanks to the French national bat monitoring program Vigie Chiro. This citizen science program based on acoustic recordings has been coordinated by the French National Museum of Natural History since 2006 (<https://www.vigienature.fr/fr/chauves-souris>). It was set up to determine bat population trends in France. It is composed of three different protocols, the data used here are those of the “stationary points protocol”, which started in 2014. In this protocol, volunteers were asked to set up ultrasonic recorders at potential bat foraging sites for at least one full-night (from 30 min before sunset to 30 min after sunrise). All recorders had to be configured with recommended settings to limit heterogeneity between devices. The recordings are processed with the bat identification software Tadarida (Bas et al., 2017). As of December 2021, the dataset based on this protocol was composed of 16,349 sampled sites and 49,909 full nights of standardised recordings made by 567 participants.

Working on such a dataset is a great opportunity because of the large number of data and their wide spatial, temporal and taxonomic range. One of its strengths is to assess the activity of several species simultaneously, so that their possible interactions are captured in the resulting dataset. Besides, it should not suffer from an observatory bias since the data are all recorded with to the same settings and as the records are processed with the same software. However, it also come with many challenges.

Indeed, volunteers upload data into the Vigie-Chiro platform to participate in the protocol but also to conduct their own research (Tadarida is currently one of the only free bat identification software). Thus, even if the “stationary points protocol” *stricto sensu* consists in carrying out surveys on randomly selected sites, during at least one full night, in good weather (no rain, no wind gusts above 30 km.h⁻¹ and mild temperature forecasted) and with two passes (the first between 15 June and 31 July, the second between 15 August and September), many surveys do not meet one or more of these requirements (this is the case of the field data we collected during this PhD and that are presented in **Box 5**). Such surveys are nonetheless valuable and might be used in many studies, but some should be discarded depending on the purpose of these studies. For instance, for Mariton et al. (*accepted*) and Mariton et al., (2022), we detected and discarded surveys that were not conducted for at least one full night, that might

Box 3: Data acquisition

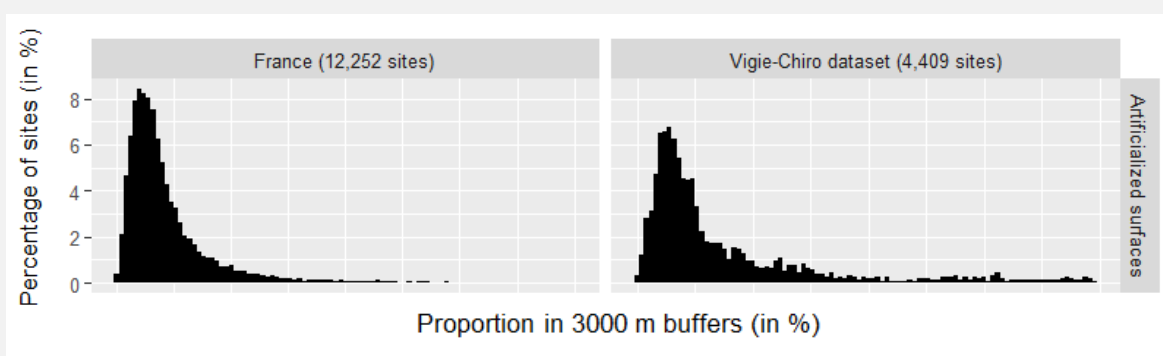
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have been carried out near a bat roost, that were conducted during inclement weather, for which we suspected abnormal settings, etc. To clean up the dataset, we wrote a set of R programs (R Core Team, 2022) that we then shared with the other researchers working on Vigie-Chiro.

Another challenge is to extract all the environmental and meteorological data needed to exploit such a large number of surveys. To do this, we had to find datasets at the relevant resolution covering at least the whole French territory and exploit them. As this was very time consuming, we chose to aggregate this work in the form of R functions in public repositories in GitHub (<https://github.com/LMariton>) so that it could be easily reused and help other researchers (among the functions available are functions allowing to extract relevant data for the study of bat activity: meteorological data such as daily temperature, wind speed, cloud cover and precipitations, landscape characteristics such as the distance to different land use types, the density of linear features in buffers around sites, the light pollution levels in buffer around sites, sunset and sunrise times for a dataset composed of nights, etc.).

Eventually, as the Vigie-Chiro program was originally designed to study bat population trends in France, the representativeness of the sampling design was a major concern. Thus, we confirmed that this representativeness was correct by checking that the buffer zones around the sites in this dataset covered the same gradients of land use type as buffer zones around randomly sampled sites in France (see *Appendix B* in Appendix I at the end of this PhD).



Gradients of the proportions of artificialized surfaces in 3000 m buffer zones around randomly sampled sites in France (every 6000 m, below 500 m above sea level) and the sites of the Vigie-Chiro dataset (below 500 m above sea level)

besides changing the spatial distribution of bats, could change their temporal one. In particular, the delay in emergence due to ALAN shown for some narrow-space-foraging bat species in localised studies (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021), could result in a reduction of the time-budget to forage for bats, and eventually alter individual fitness or even population dynamics. Despite, these potential dramatic effects of light pollution on bats, there is a lack of studies on whether **light pollution can disrupt bat diel activity pattern**, in particular at their foraging sites and for species that are usually considered to be “light tolerant”.

In the second chapter of this PhD, we first focused on a “light tolerant” species, *E. serotinus*, which is known to forage under streetlights but also to have a lower activity due to ALAN at the landscape scale. We intended to answer the following questions:

- (1) At the national scale, is the activity of a “light tolerant” species lower because of light pollution?**
- (2) If so, does light pollution affect the diel activity pattern of this bat species at foraging sites and to what extent?**

Limiting light trespass and reducing light intensity are two complementary measures that could be implemented to reduce light pollution effects on biodiversity. Thus, determining whether there is **a threshold of intensity below which light ceases to affect bats** would be of utmost interest. However, the effects of diffuse low light levels – similar to those due to skyglow or moonlight – have been little studied for bats, especially in temperate regions. Thus, we also intended to answer the following question:

- (3) Can small variations in light levels have an impact on the spatiotemporal activity pattern of a light “tolerant species”?**

This study has been published in 2022 in *Environmental Pollution*:

- **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. *Environmental Pollution* 305, 119267.
<https://doi.org/10.1016/j.envpol.2022.119267>

While the results of this study provide new insights on the impact of light pollution on bat species, there is still a need to **assess whether such results can be expanded to other**

insectivorous bat species. Thus, we presented preliminary analyses on other temperate open- and edge-space-foraging species usually considered to be “light tolerant”.

Where and when it is not possible to switch off lights, modifications of the technological characteristics of light (i.e. reduction of intensity, trespassing and choice of an appropriate light spectra) could help to mitigate light pollution impacts on biodiversity. As obsolete lighting equipment are progressively phased out and replaced by LEDs in developed countries, assessing the impact on biodiversity of the modification of the spectrum of ALAN is of utmost importance. As a matter of fact, it has been shown that a wide range of biological responses to light pollution, both behavioural and physiological, are sensitive to the spectrum of the emissions (Sánchez de Miguel et al., 2022). Thus, the broad spectrum of **LEDs has the potential to alter many organisms and processes** compared to previous lighting equipment such as LPS lamps which only emit a narrow-band spectrum (**Figure 3**).

However, to date, not much studies have investigated the effect of switching from old lighting technologies to LEDs. While two studies found a reduction in the activity of some bat species when switching from MV lamps to LEDs (Haddock et al., 2019b; Lewanzik and Voigt, 2017), one study in the tropics found no effect for the switch from HPS lamps to LEDs (Lee et al., 2021) and another in England found no effect for the switch from LPS to LEDs (Rowse et al., 2016). However, when studying the impact of a switch of lighting technologies, we need to consider all lighting characteristics that are changed. In particular, **intensity is an important factor to consider when studying bat responses to light pollution** (Hale et al., 2015; Stone et al., 2015b) and, as explained above, the higher luminous efficiency of LEDs could lead to a “rebound effect” resulting in a greater use of light in terms of spatial extent and intensity (Kyba, 2018; Sánchez de Miguel et al., 2022).

Thus, in the third chapter of this PhD, we presented a reanalysis of Rowse et al. (2016) data that answers the following questions:

- (1) Does the switch from LPS lamps to LEDs impact bat activity?**
- (2) Is bat activity influenced by the interaction between light intensity and emission spectrum?**

The results of this reanalysis have been published in 2022 in *Diversity*:

- Kerbiriou, C., Barré, K., **Mariton, L.**, Pauwels, J., Zissis, G., Robert, A., Le Viol, I., 2020. Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of Bats. *Diversity* 12, 165. <https://doi.org/10.3390/d12040165>

Furthermore, as **ALAN alters the functional connectivity for bats across urban areas** where landscapes are already highly fragmented (Laforge et al., 2019), the switch in spectrum may have dramatic consequences for these species. Assessing the potential impact of the transition to LEDs on landscape connectivity is therefore an urgent need. However, so far, no study has done so. I thus presented a study in preparation (Pauwels et al., *in prep*)) focusing on three French cities, which aims to answer the following questions: **How the predicted transition from conventional lighting equipment to LEDs will affect landscape connectivity for bats? Will this change in lighting technology have different impact according to the city considered? Can the dimming of streetlights (i.e. better directing the light flux of the LEDs) help reduce the potential negative impact of LEDs on bats?**

Eventually, in order to move on to new ways of lighting (or not lighting), we need to understand the complexity of the network of actors involved in ALAN and to consider the relationship that we, both living humans and non-humans, have with darkness. It is thus necessary to adopt a transdisciplinary perspective, hence the initiation of a project on public lighting practices in municipalities that we presented in the general discussion of this PhD.

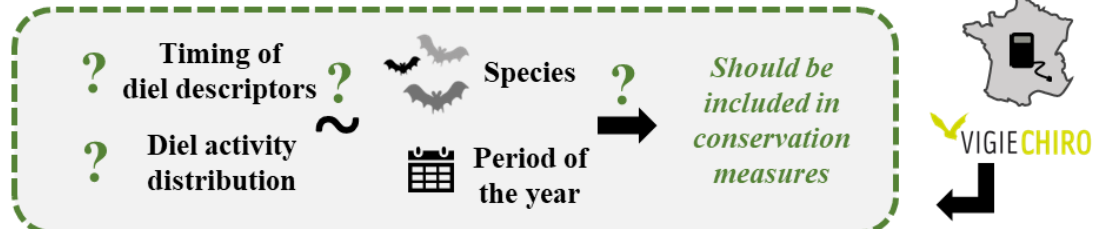
A graphical plan of this PhD can be found **Figure 8**.

Chapter 1: Taking diel activity patterns into account in conservation measures



- *Objective*: characterising the diel activity patterns of bat species so that their consideration in mitigation measures can help conservation

QUESTIONS



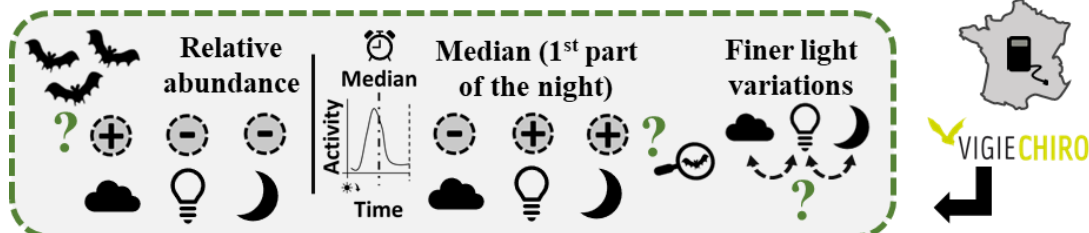
Mariton et al. (accepted)

Chapter 2: Impact of light pollution on bat diel activity patterns



- *Objective*: assess whether light pollution affects the timing of activity of bats at their foraging sites, at landscape scale

QUESTIONS



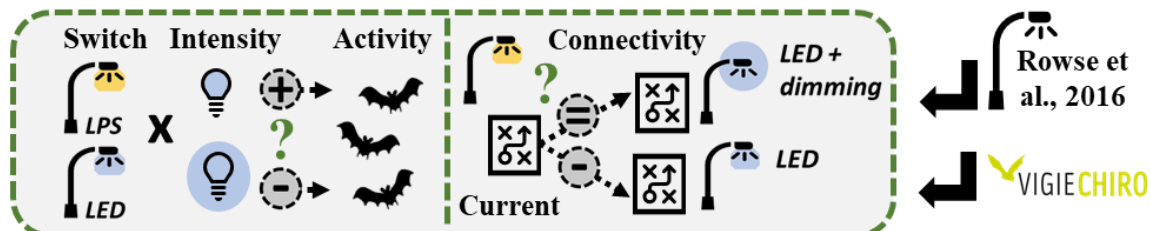
Mariton et al. (2022)

Chapter 3: Are technological developments in lighting threats to bats?



- *Objective*: assess whether the switch from conventional lighting to LEDs may pose a threat to bat species

QUESTIONS



Kerbiriou et al. (2020)

Pauwels et al. (in prep)

Figure 8: Plan of the PhD: objectives and questions

Chapter 1: Taking diel activity patterns into account in conservation measures

“Notre arbre était à présent envahi par les chauves-souris qui entonnèrent un chant. Leurs voix aigües, vibrantes, heurtaient les particules de la brume, et la nuit autour de nous s’était mise à résonner doucement d’un son de cloche, appelant ainsi toutes les créatures à célébrer une messe nocturne.”

Olga Tokarczuk, Sur les ossements des morts

Based on the publication:

Mariton, L., Le Viol, I., Bas, Y., Zanda, B., Kerbirou, C., 2022. Characterising diel activity patterns to design conservation measures: case study of European bat species.

(accepted in Biological Conservation)

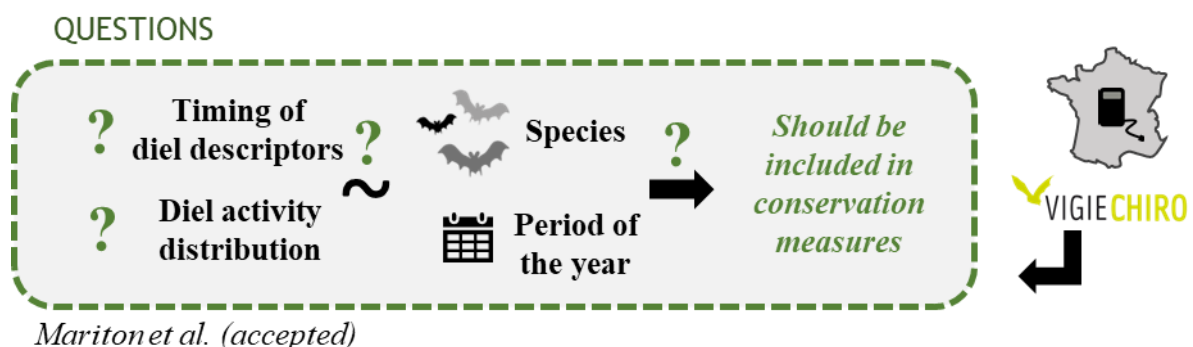


Figure 9: Questions of the first chapter

Context

PNL is increasingly being implemented by municipalities in Europe (Bennie et al., 2014a). Such a measure allows to save energy and reduce costs associated with ALAN in response to economic pressures, limited energy supplies and/or efforts to reduce energy consumptions and greenhouse gas emissions (Gaston et al., 2013). PNL is also one of the principal levers proposed to mitigate the adverse effects of light pollution on biodiversity.

To date, very few studies focused on the effectiveness of PNL in reducing the impact of ALAN on ecosystems. Azam et al. (2015) showed that PNL could fail to fully reduce the impact of ALAN on bats, indeed they found no significant effect of PNL on the activity of six of the eight bat species studied compared to full-night lighting (*Myotis* spp., *P. kuhlii*, *Pipistrellus nathusius*, *Nyctalus leisleri*, *E. serotinus*). Similarly, Hooker et al. (2022) did not find significant effect of PNL on the activity of two of the four bat species groups studied (*P. pipistrellus* and the *Nyctalus/Eptesicus* spp. group) compared to full-night lighting. This lack of effect on many bat species could be due to the fact that some species could adapt their foraging strategy according to the lighting present at the beginning of the night (without then returning to potential foraging sites where light could have been switched off in the middle of the night) and/or the fact that PNL schemes do not overlap with the range of activity of these bat species (Azam et al., 2015).

As advocated by Day et al. (2015) in their study on the diel activity pattern of *R. ferrumequinum*, the diel activity pattern of target bat species should be taken into account when planning when the lights will be switched off in the evening and switched on in the morning. However, to date, knowledge on the diel activity patterns of insectivorous bats is scattered in the scientific and grey literature and it is almost solely based on local scale studies and biased toward emergence from roosts. Some authors, like Erkert (1982) and Jones and Rydell (1994) tried to synthesised this scattered knowledge in valuable reviews. However, they are based on studies of limited taxonomic, spatial and temporal ranges.

The development of passive acoustic monitoring (PAM) and automated identification software coupled with the emergence of citizen science program now allow to collect data on bat activity at wide scales. In particular, Newson et al., (2015) showed that citizen science programs based on PAM offer great opportunities to provide new insights in bat temporal ecology. In this first chapter, we therefore used the data from the French bat monitoring program based on citizen science and standardised acoustic recordings to characterise the diel

activity patterns of 20 bat species (out of the 36 species that can be found in France) so that their consideration in mitigation measures can aid conservation.

We intended to answer the following questions (**Figure 9**):

(1) Can we distinguish functional groups of bat species to inspire multi-taxa approaches in conservation based on diel activity patterns?

In particular, in accordance with Jones and Rydell (1994) review on emergence time from roosts, we predicted that bat diel activity patterns will be determined by a trade-off between energetic needs and predation risks. We predicted that species that have a fast and agile flight and that forage on small insects whose activity peaks at dusk and dawn would have a crepuscular activity. Conversely, we predicted that species with a low and slow flight, feeding on moths or flightless prey would tend to forage outside of dusk and dawn.

(2) Should conservation measures take into account the variations in bat diel activity patterns according to the period of the year?

In accordance with previous localised studies (e.g. Robinson and Stebbings, 1997; Swift, 1980), we predicted that if the temporal niche of bat species was indeed determined by a trade-off between energetic needs and predation risks, then variations in energy demands throughout their reproduction cycle (e.g. highest energetic needs for reproductive females during lactation (Racey and Speakman, 1987)) would lead to variations in their diel temporal activity patterns.

It has been suggested that to address conservation issues, biological conservation must be holistic, considering multiple spatial and temporal scales (Lindenmayer and Hunter, 2010). However, although diel activity time is a major axis of species' niche space, very few conservation measures focus on preserving daily periods free of anthropogenic pressures. Throughout this chapter, we thus intended to illustrate how this synthesised knowledge of bat diel activity patterns can be integrated not only in PNL schemes but also into other pre-existing conservation measures such as wind turbine curtailment.

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Characterising diel activity patterns to design conservation measures: case study of European bat species

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Highlights

Conservation should include species temporal distribution besides their spatial one.

Citizen science programs enable the study of bat diel activity patterns at wide scales.

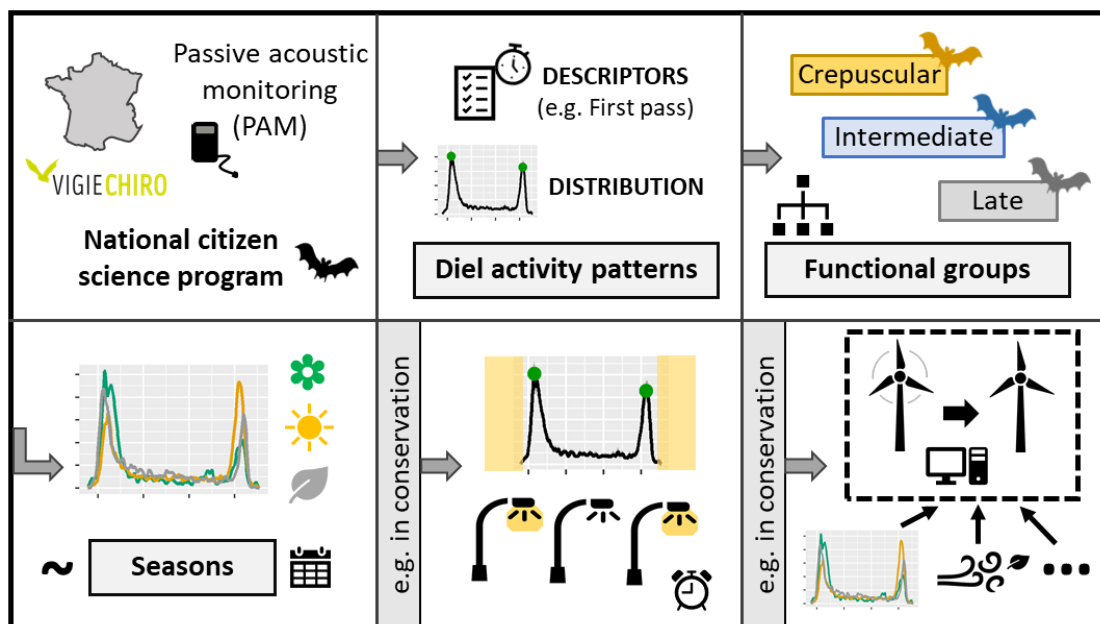
Similarities in diel activity patterns of bats enable functional groups to be defined.

Seasons can interact with the time of night to determine diel activity patterns.

Diel activity patterns should be considered when designing efficient mitigation measures.

Abstract (Figure 10)

Although diel activity time is a major axis of species' niche space, very few conservation measures focus on preserving daily periods free of anthropogenic pressures. While the spatial ecology of bats has received much attention, less is known about their temporal ecology, the knowledge being dispersed in studies of limited taxonomical, spatial and temporal range. We used data from the French bat monitoring program based on citizen science and standardised acoustic recordings (4409 sites monitored and 9807 nights monitored from 2014 to 2020) to characterise the diel activity patterns of 20 bat species so that their consideration in mitigation measures can help conservation. We designed a method to extract times of key descriptors and describe bat activity distribution throughout the night. We found that bat species could be separated in three functional groups characterised by a crepuscular activity, an activity that occurs when it is completely dark or an intermediate activity. We showed variations of diel activity patterns depending on season. We argue that accounting for these complex diel activity patterns would help design efficient mitigation measures, for instance to reduce the exposure of bats to light pollution or wind turbines. Overall, we advocate multi-taxa approaches to design conservation policies adapted to both the temporal and spatial distributions of species.

**Figure 10:** Graphical abstract of Mariton et al. (*accepted*)

1. Introduction

To address conservation issues, biological conservation must be holistic, considering multiple spatial and temporal scales (Lindenmayer and Hunter, 2010). Spatial ecology has developed to meet this challenge and guide conservation measures from local to global scales (e.g. from the designation of local reserves to the rationalised designation of networks of protected areas and corridors). Space protection has fit in (inter)national regulations and global discussions (e.g. National park designation, Natura 2000 network, Aichi biodiversity target of 17% of terrestrial surfaces protected by 2020). Conversely, and despite the importance of time in shaping ecosystems, temporal ecology has received much less attention (Wolkovich et al., 2014).

Since anthropogenic changes can alter temporal dynamics of ecosystems at various scales, protecting time should be as important a concern as protecting space. However, conservation measures explicitly based on the temporal ecology of species are mainly implemented at local spatial scales, most are incentives rather than regulations and they generally focus on the annual scale (e.g. changing timing of building work to avoid bat hibernation and maternity season, delaying mowing in pastures to protect chicks and nests of ground-nesting birds, prohibiting hunting of species during reproduction, etc.) (Sutherland et al., 2021). In contrast, finer temporal scales are more rarely accounting for in conservation measures.

Although diel activity time is a major axis of species' niche space (Schoener, 1974), very few conservation measures focus on preserving daily periods free of anthropogenic pressures. In response to the 24-hour periodicity of their environment, living organisms have developed endogenous circadian rhythms entertained by exogeneous influences (e.g. temperature and light-dark cycles) (Aschoff, 1989; Erkert, 1982). These mechanisms allow them to occupy a given temporal niche and coordinate their activity with that of other organisms with which they interact (e.g. conspecifics, predators, prey) (Aschoff, 1989; Erkert, 1982). Time of high species activity should hence be protected to preserve biodiversity at multiple scales, from individual fitness to ecosystem functions.

The very few conservation measures focusing on sharing daily time between human activities and biodiversity tend to be based on the times when human needs are lowest rather than on the diel activity patterns of species. For instance, part-night lighting (PNL, i.e. switching off public lighting during the middle of the night) aims to reduce light pollution impacts on biodiversity (Gaston et al., 2012). However, current PNL schemes are not efficient enough as they do not encompass the range of activity of nocturnal species such as bats (Azam et al., 2015;

Day et al., 2015; Hooker et al., 2022). Similarly, algorithm-based curtailment of wind turbines aims to reduce bat fatalities while minimising energy production losses. The most widespread curtailment strategy is only based on a windspeed threshold below which the turbine is curtailed due to expected high bat activity. While curtailment has been shown to be efficient, its results remain variable and it does not fully reduce fatalities (Adams et al., 2021; Whitby et al., 2021). Its efficacy would benefit from considering other variables impacting bat activity such as diel activity time (Behr et al., 2017; Friedenberg and Frick, 2021). To include diel activity patterns in conservation measures, a general knowledge on species' temporal distribution, based on standardised and comparable metrics, should be available, which is not the case so far for taxa like bats.

As European bats are a diversified group mainly composed of long-lived insectivorous species occupying high trophic levels, it has been suggested that they can be good bioindicators of the effects of anthropogenic pressures and mitigation measures on biodiversity (Jones et al., 2009; Russo et al., 2021). However, while the spatial ecology of bats has received much attention (e.g. Laforge et al., 2021) less is known about their diel activity patterns, knowledge being dispersed in literature. Most studies informing on diel activity patterns are monospecific and the patterns of many European species have received little to no attention (e.g. *Myotis emarginatus*, *Tadarida teniotis*) (see Appendix A for an overview of the scientific literature). Existing studies have almost all been conducted at local spatial scales (however, at large scales see Day et al., 2015; Mariton et al., 2022; Newson et al., 2015) and they tend to be biased toward monitoring emergence at roosts. Some authors showed that diel activity patterns can vary throughout the year, rising the need for studies conducted at large temporal scales (e.g. Robinson and Stebbings, 1997; Swift, 1980).

The dispersed knowledge on bat diel activity rhythm could be synthesised in a review as Jones and Rydell (1994) did for the time of emergence. However, it would be based on a small number of papers with limited taxonomical, spatial and temporal scope. It would not encompass environmental gradients within species' range and would not provide comparable data between species. In comparison, citizen science coupled with technological developments (e.g. acoustic monitoring, computer vision) offers great opportunities to monitor biodiversity at unprecedented spatiotemporal scales (Newson et al., 2015; van Klink et al., 2022). Newson et al. (2015) showed, at a regional scale, the potential for public contribution to provide new insights into the temporal ecology of bats.

Ecologists lack a unified method to describe bat diel activity patterns. In some studies (e.g. Day et al., 2015; Hooker et al., 2022; Newson et al., 2015), they were characterised by a

level of activity during time periods (e.g. every hour). While this method can provide an overview of the activity distribution throughout the night, it discretises continuous time series and implies to choose a time period that maximize precision (i.e. shortest periods possible) without flattening activity patterns (i.e. enough activity per period). Other authors focused on times of “key descriptors”, such as the time of first or median emergence (Bullock et al., 1987; Jones and Rydell, 1994). It enables to not discretise time series, but it does not describe the activity distribution throughout the night. These methods appear to be complementary by providing different information on the temporal ecology of bats.

We used data from a citizen science bat monitoring program – based on standardized acoustic monitoring throughout France (4409 sites monitored and 9807 nights monitored from 2014 to 2020) – to characterise the diel activity patterns of 20 bat species. Through the calculation of the times of key descriptors and the representation of the activity distribution throughout the night, we aimed to provide a synthetic and general knowledge on bat diel activity patterns. This knowledge could be used in conservation, for instance, to distinguish functional groups of species that could inspire multi-taxa approaches or to pave the way for the consideration of variation of diel activity patterns throughout the year to design efficient conservation measures. In particular, we predicted that (1) the overall diel activity patterns of bat species will be driven by their diet and foraging strategies along with their ability to avoid predation, (2) that bat diel activity patterns will vary throughout the year according to their reproduction phenology.

2. Materials and methods

2.1. Biological data

We used data from the “stationary points protocol” of the French citizen science bat monitoring program Vigie-Chiro (coordinated since 2014 by the French National Museum of Natural History, <https://www.vigienature.fr/fr/chauves-souris>) (see Appendix B for details on data acquisition and curation). Volunteers were asked to set up ultrasonic recorders on potential bat commuting/foraging sites for at least one full-night. We used data from 9807 monitored nights on 4409 sites. Preliminary analyses ensured that the monitored sites covered similar land-use gradients as randomly selected sites in France.

We considered bat passes, defined as the occurrence of a single or several bat calls during a 5-s interval (Millon et al., 2015) as a proxy for activity. Species identification was

performed with the Tadarida software which classifies bat passes into classes according to a confidence index value (Bas et al., 2017). We only kept passes with a confidence index value greater than 0.5, to obtain, for each species, a maximum error rate tolerance (MERT) of 0.5. *Myotis blythii* and *Myotis myotis* were grouped in a complex named Great *Myotis* because of their high acoustic similarity (Barataud, 2020). Species for which there were not enough data (i.e. in less than 200 sites after data curation) and species for which we considered that automatic identification was not robust enough were discarded. Eventually, we studied 20 species. To ensure result robustness against automated identification errors that could persist despite the precautions we took when filtering and analysing the data, we chose to follow the approach of Barré et al. (2019) (Appendix C). We showed that our results were not sensitive to the error rates considered and were robust against automated identification errors.

2.2. Characterisation of the diel activity patterns

2.2.1. Key descriptors

First, we characterise diel activity patterns by defining “key descriptors” within nights. Indeed, descriptors such as the time of emergence has been related to reproduction success (Boldogh et al., 2007; Duvergé et al., 2000). We considered the percentage of the night elapsed (R 4.2.0 (R Core Team, 2022), R package *StreamMetabolism* (Sefick, 2016)). Indeed, we could not use raw time to characterise diel activity patterns as bat activity tends to be parallel to sunset and sunrise times (Erkert, 1982) and as, in our large-scale dataset these times are variable according to the period of the year, latitude and longitude. Hours after sunset have been used in some studies (e.g. Day et al., 2015; Jones and Rydell, 1994; Newson et al., 2015). However, considering hours after sunset as a measure of time does not correct for the variable time of sunrise. In comparison, the percentage of the night elapsed allows the sunset time to always be equal to zero and the sunrise time to 100.

We calculated the time of five “key descriptors” for each species: (i) the time of the median pass (TMedian), (ii) the time of the first pass (TFirst) and the median pass (TMedianP1) during the first part of the night, (iii) the time of the last pass (TLast) and the median pass (TMedianP2) during the second part. TFirst and TLast rely on a single pass and are vulnerable to extreme values, however they provide information on the start and the end of activity independently of the overall activity pattern. Conversely, TMedian, TMedianP1 and TMedianP2 are less influenced by extreme values and provide information on the overall

activity pattern. We considered the medians during each night half because previous studies showed that diel activity patterns of insectivorous bats tend to be bimodal with a first activity peak after sunset and a second, weaker, before sunrise (Erkert, 1982).

We calculated an overall value for the time of each key descriptor (hereafter called the “mean” value) following the workflow presented in (**Figure 11**). To account for the hierarchical structure of the dataset, we calculated (i) the times of the key descriptors by night, then (ii) the mean times by site (we applied a weight based on the number of passes by night as we postulated that the more passes there are during a night, the more robust the estimation of the times of the key descriptors), eventually (iii) the mean times over the whole dataset using the mean times by site (we applied a weight based on the mean number of passes by sites) (Appendix D).

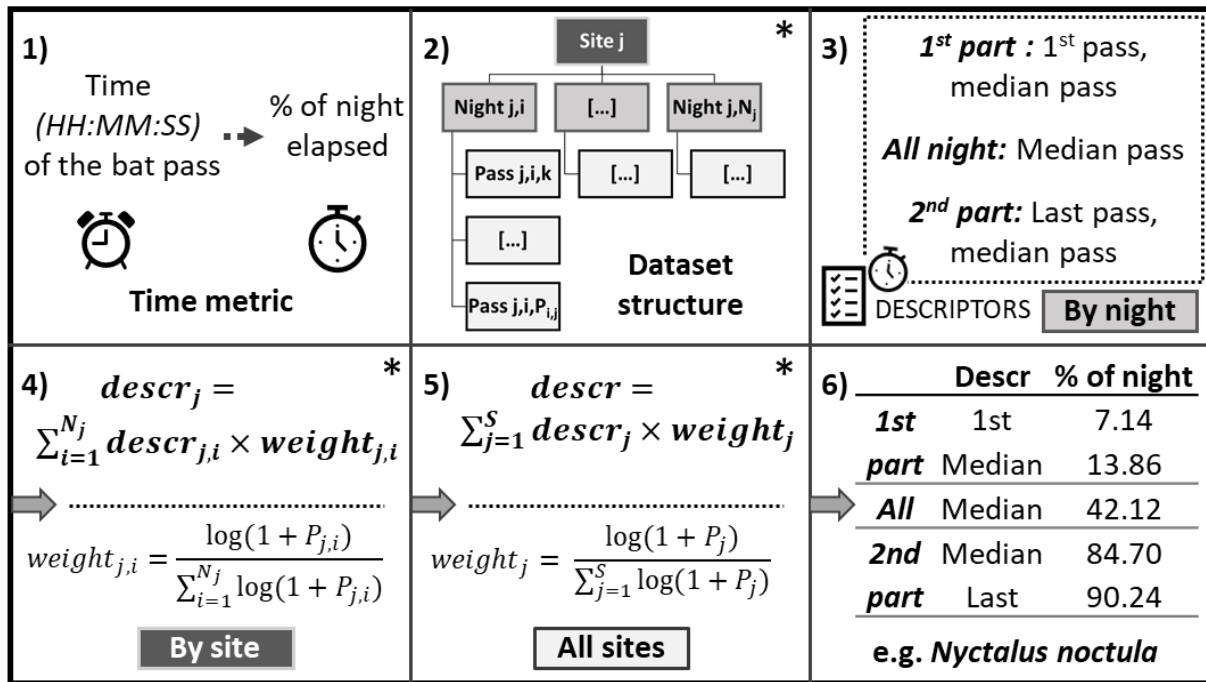


Figure 11: Schematic process for the calculation of the times of key descriptors. Preliminary information (1-2), method implemented (3-5), example of the mean values for *Nyctalus noctula* (6).

* j = site ID; i = i^{th} night of a site; k = k^{th} pass in a night; S = number of sites; N_j = number of surveyed nights at the site j ; $P_{j,i}$ = number of passes of the night j,i ;

$descr$ = time of the descriptor;

P_j = “mean” number of passes of the site j = $[\sum_{i=1}^{N_j} P_{j,i} \times \log(1 + P_{j,i})] / [\sum_{i=1}^{N_j} \log(1 + P_{j,i})]$

2.2.2. Activity distribution throughout the night

Secondly, we assessed the activity distribution throughout the night by calculating an estimated density of activity (R function *density*) (see Appendix D). In previous studies (e.g. Day et al., 2015; Newson et al., 2015), some authors considered the number of bat passes during given time periods (e.g. every hour). In comparison, density estimation allowed to better account for the continuous aspect of our data.

We followed the workflow presented in (**Figure 12**). We used all the passes of each species as, for rare species particularly, there were not enough passes to characterise the activity distribution by night. We accounted for the hierarchical structure of our dataset by assigning a weight to each pass so that (i) the weight of a site in the density calculation was based on the mean the number of passes of this site, (ii) the weight of a night within a site was based on the number of passes of this night, (iii) each pass of a night within a site had the same weight. We calculated 95% confidence bands for the estimated densities using bootstrap (1000 resamples). We defined the times of activity peaks (TPeakP1 and TPeakP2 for peaks occurring during the first part and the second part of the night respectively) as the times of local density maxima with a high peak score (a high peak score meaning that the distance between the density value at a time point was high compared the density values surrounding it) (R package *scorepeak* (Ochi, 2019)).

We calculated a cumulative curve of weighted bat activity throughout the night using the cumulative weight of all passes ranked by increasing percentage of the night elapsed. To assess whether the weighted activity of a species was concentrated around activity peaks or more evenly distributed throughout the night, we searched for the 15 % interval of the night during which its weighted activity was maximum and we calculated this maximum.

2.3. Examples of comparison of diel activity patterns inter- and intra-species

2.3.1. Activity distribution throughout the night according to the season

To assess variations of activity distribution throughout the night according to the season, we estimated the densities of activity on subsets of our datasets. Indeed, some authors showed that bat diel activity patterns could change according to their reproductive states (e.g. Robinson and Stebbings, 1997; Swift, 1980). We applied the density calculation method to three temporal subsets: spring (1 March to the 21 June, 1447 sites, 2762 nights), summer (22 June to 21 August, 2448 sites, 4373 nights) and autumn (22 August to 31 October, 1342 sites, 2642 nights). In

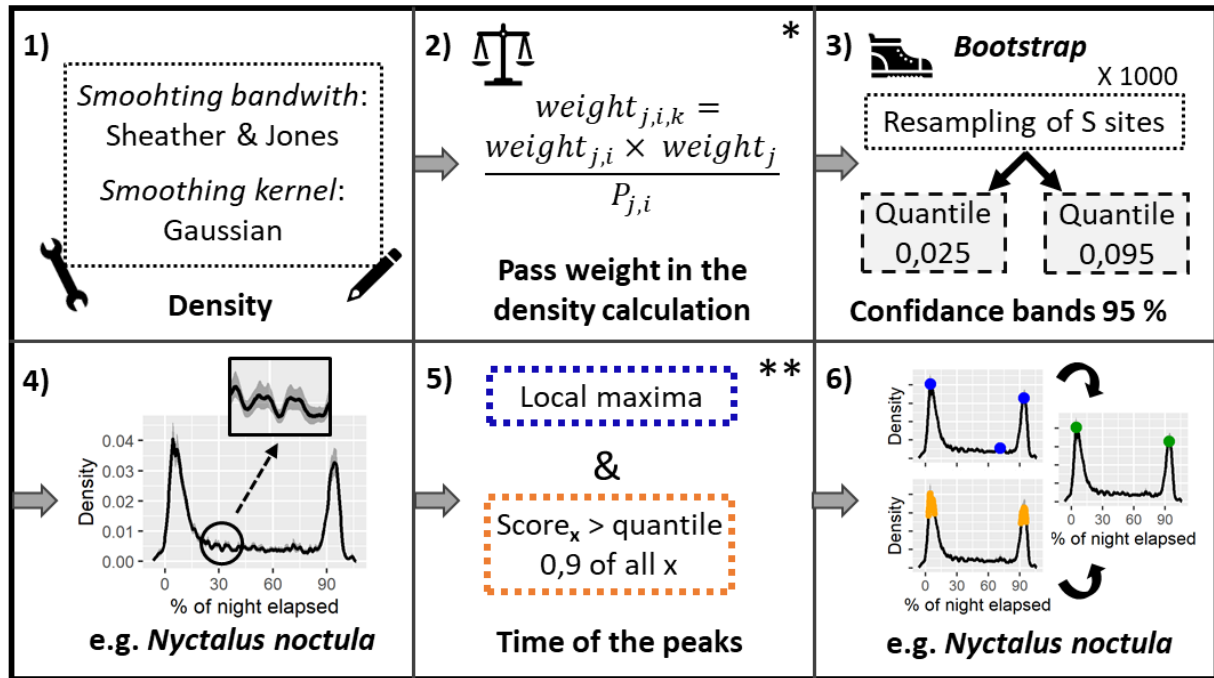


Figure 12: Schematic process of the characterisation of the activity distribution throughout the night: calculation of a density (1-2), calculation of the confidence bands (S being the number of sites in the dataset for the species considered), (3) example: activity pattern of *Nyctalus noctula* (4), extraction of the time of the activity peaks (5), example: peak detection for *N. noctula* (6).

* see legend **Figure 11**

** For local maxima and score calculation, window of temporal neighbours = 129 (i.e. 1/4 of the night); x = percentage of night elapsed discretised;
score_x = density_x – mean (density of the temporal neighbours)

France, for most species, these periods corresponded approximately to the hibernation ending/gestation, lactation and dispersion/reproduction (Arthur and Lemaire, 2015).

2.3.2. Clustering of the species

To determine whether species could be clustered in functional groups according to similarities in their diel activity patterns, we performed a Hierarchical Clustering on the Principal Components (HCPC) of a Principal Component Analysis (PCA) (R package *FactoMineR* (Lê et al., 2008)), the variables used being the times of the keys descriptors and the times of the activity peaks. For each variable, we calculated the difference between the average for the species in a cluster and the overall average (i.e. the average for all species studied). We tested whether the average in each cluster was equal to the overall average (Husson et al., 2010, 2009).

3. Results

3.1. Diel activity pattern description

The mean time of the key descriptors and the time of the activity peaks varied greatly according to the species (**Figure 13**, Table E and Figure G). We did not detect any activity peak for *Myotis mystacinus* and *Plecotus auritus*. For six species, we detected a unimodal activity pattern with a single activity peak in the first part of the night (*Barbastella barbastellus*, *Eptesicus serotinus*, the Great *Myotis* *Myotis daubentonii*, *Pipistrellus nathusii* and *Plecotus austriacus*). For the remaining 12 species, we detected a bimodal activity pattern with one peak during the first part of the night and another during the second. As the times of the peaks were extracted from the estimated density using all weighted passes they are not directly comparable to the times of the key descriptors calculated as successive weighted means by night and site.

The activity distribution throughout the night varied substantially according to the species (**Figure 14** and Figure H). For instance, the 15 % interval of the night with the most activity occurred at the beginning of the night and included the TFPeak for all species for which we detected an activity peak (except for *T. teniotis*). However, the percentage of weighted activity during this interval varied from 17.4 % for *M. emarginatus* – whose activity is almost uniformly distributed – to 43.1 % for *Hypsugo savii* – whose activity is strongly condensed into peaks (Table I). Some species were more crepuscular than others: for instance, 54 % of the weighted activity of *Nyctalus noctula* occurred before 10 % of the night had elapsed and after 90 % of the night had elapsed, compared to only 7.7 % of the weighted activity of *P. auritus*.

3.2. Clustering of species according to their temporal niche

The species clustering resulted in three clusters (**Table 1**, Appendix J). The first cluster, composed of *Pipistrellus pipistrellus*, *Pipistrellus pygmaeus* and *N. noctula* was characterised by an earlier activity at the beginning of the night and a later activity at the end, we called the species in this group “crepuscular” species. The second cluster was composed of ten species: the Great *Myotis*, *P. auritus*, *M. emarginatus*, *Myotis nattereri*, *P. austriacus*, *Rhinolophus hipposideros*, *M. mystacinus*, *T. teniotis*, *B. barbastellus* and *Miniopterus schreibersii*. It was characterised by a later activity at the beginning of the night and a sooner end of activity at

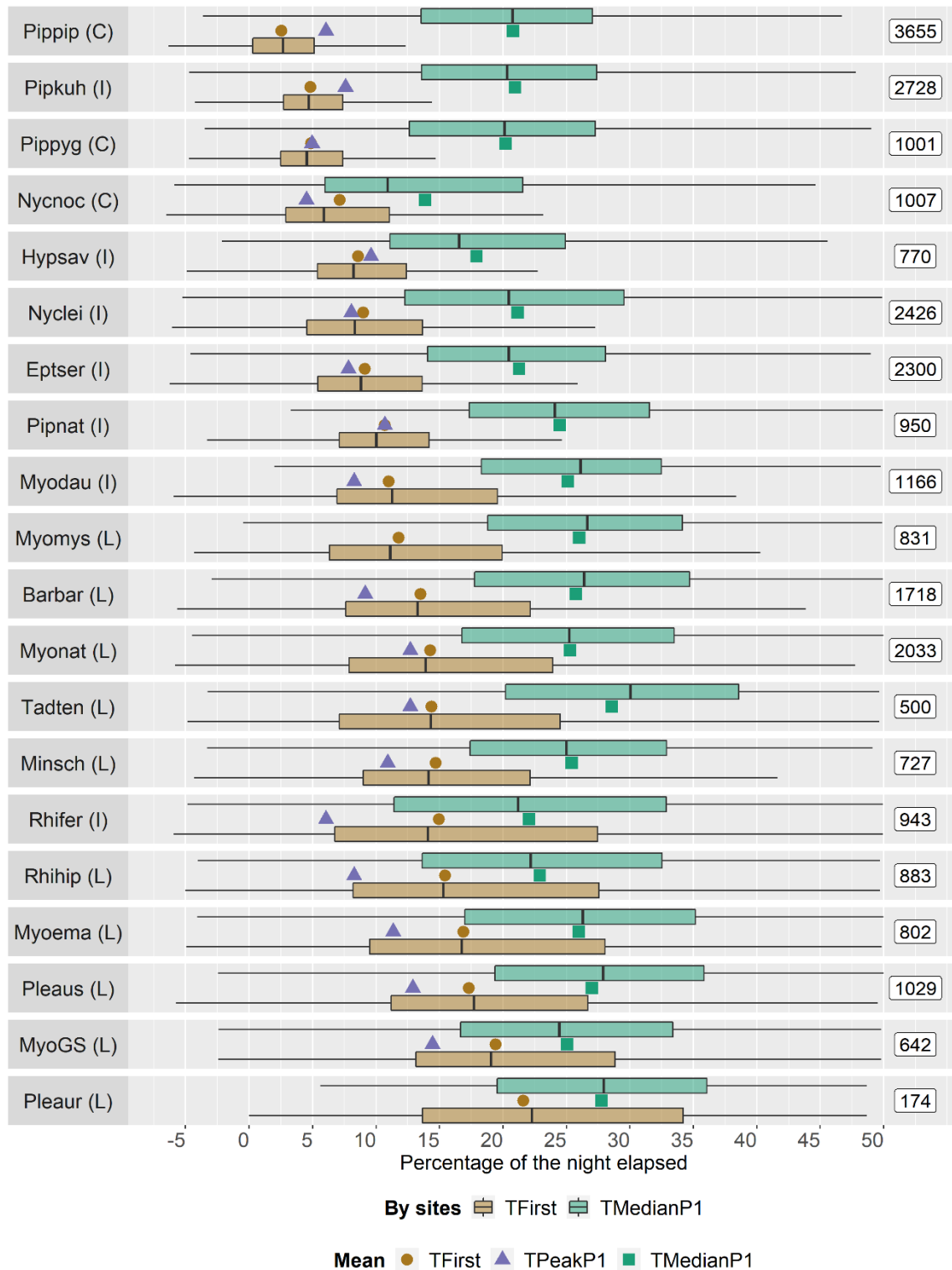


Figure 13: TFirst, TPeakP1 and TMedianP1 for each bat species.

On the left are the codes of the species studied (correspondence between the codes and the full Latin and English names in Table F), followed by the cluster in which they were classified according to the HCPC (C: crepuscular species, I: intermediate species, L: late species). On the right is the number of sites monitored by species. Species are ranked by increasing value of mean TFirst. For *Pipistrellus pygmaeus* (Pippyg) and *Pipistrellus nathusii* (Pipnat) the mean TPeakP1 and TFirst were almost equal.

The end, we called species in this group “late” species. The last cluster was composed of seven species: *Pipistrellus kuhlii*, *H. savii*, *E. serotinus*, *M. daubentonii*, *P. nathusii*, *Nyctalus leisleri* and *Rhinolophus ferrumequinum*. These species had an activity at the beginning and the end of the night intermediate between those of the “crepuscular” and “late” species, with an average TMedian that was significantly earlier than the average considering all species. We called species in this group “intermediate” species.

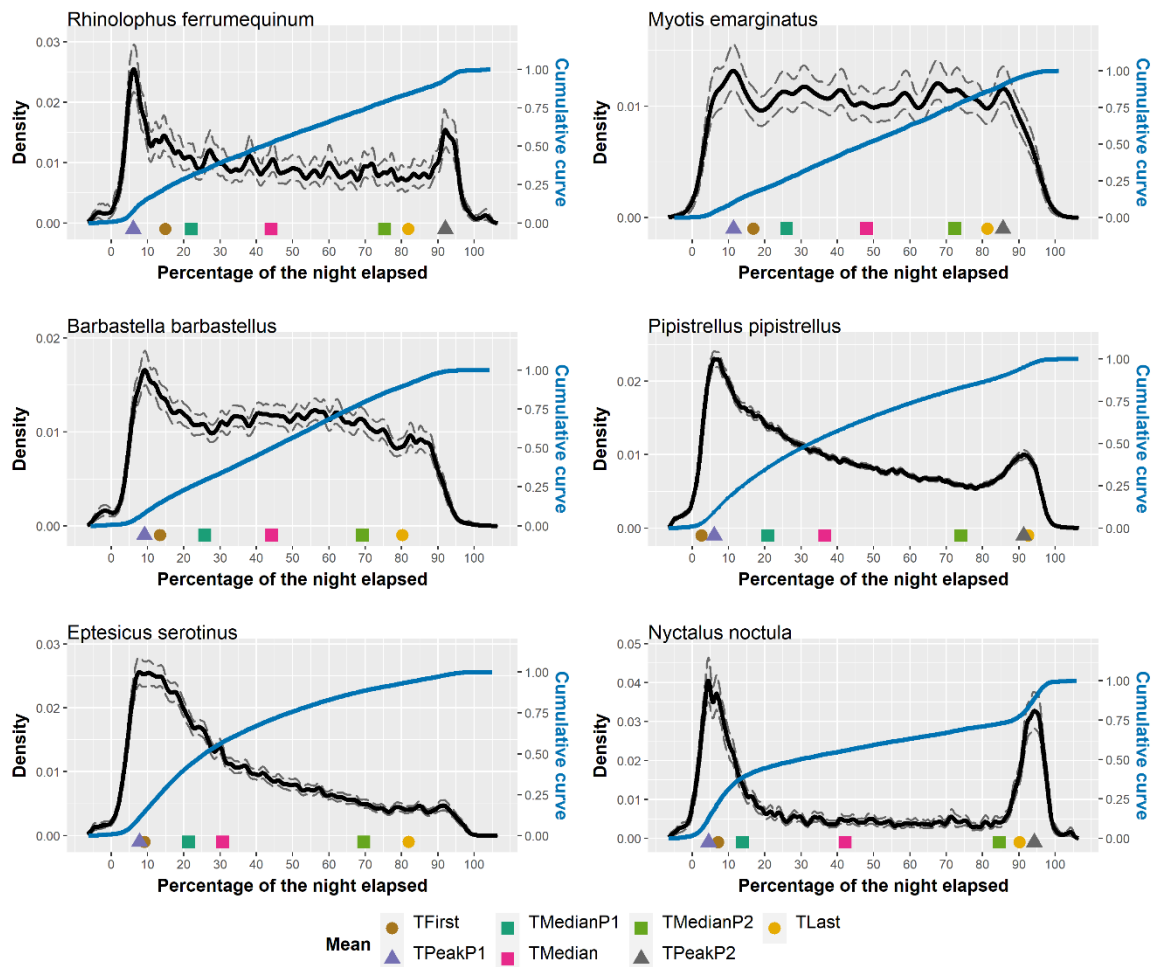


Figure 14: Activity distribution throughout the night for six species in black, estimated density of activity according to the percentage of the night elapsed. In blue, cumulative curve of weighted bat activity. The dashed lines represent the 95 % confidence bands for the estimated density. Symbols represent the mean times of the key descriptors and the times of the activity peaks detected.

Table 1: Description of the clusters. “Average cluster” and “Overall average” correspond to the average of the variables (mean times of the key descriptors or times of the activity peaks) for the species in the cluster and for all species respectively. “p.value” is the p-value obtained by testing the hypothesis: “the average of the cluster is equal to the overall average”. Only variables for which the p-value was lower than 0.05 for the cluster are shown. “Diff in %” is the difference between the average in the cluster and the overall average in percentage of the night elapsed. “Diff in min” is the difference in minutes for a nine-hour night.

Cluster	Key descriptors	Average cluster	Overall average	Diff in %	Diff in min	p.value
Crepuscular	TLast	91.5	83.7	7.8	42.2	0.0016
	TMedianP2	78.2	72.7	5.5	30.0	0.0034
	TPeakP2	92.7	85.8	6.9	37.2	0.0368
	TPeakP1	5.2	9.7	-4.5	-24.2	0.0097
	TMedianP1	18.3	23.4	-5.1	-27.5	0.0081
	TFirst	4.9	12.1	-7.2	-39.1	0.0072
Intermediate	TMedian	37.0	41.7	-4.7	-25.3	0.0078
Late	TFirst	15.9	12.1	3.8	20.7	0.0007
	TMedianP1	26.0	23.4	2.6	14.0	0.0013
	TPeakP1	12.0	9.7	2.3	12.4	0.0016
	TMedian	45.6	41.7	3.9	21.3	0.0023
	TLast	80.8	83.7	-3.0	-15.9	0.0046
	TPeakP2	81.5	85.8	-4.4	-23.6	0.0016

3.3. Variations of the activity distribution throughout the night according to the seasons

Despite slight variations, the times of the activity peak and the activity distributions throughout the night remained generally similar across all seasons (**Figure 15**, Figure K). However, for some species, the amplitudes of the activity peaks changed between seasons (e.g. weak and widespread activity peak at the beginning of the night for *E. serotinus* in summer, compared to thinner and stronger peaks during other seasons). For some species, activity peaks were not even detectable during some periods (e.g. strong activity peak at the beginning of the night for *B. barbastellus* in spring, compared to weak or even non-detectable peaks during other seasons).

Bats tended to be proportionally more active at the end of the night in summer. For all

species (except for the Great *Myotis*), the percentage of weighted activity occurring after 80 % of the night had elapsed was greater in summer than in other seasons (considering all species, mean difference of weighted activity between summer and spring: 4.6 %, between summer and autumn: 6.3%). The percentage of weighted activity occurring after 80 % of the night had elapsed was also greater in spring than in autumn for 15 species out of 20 (mean difference of weighted activity between spring and autumn: 1.6 %).

Conversely, bats tended to be proportionally less active at the beginning of the night in summer. For all species (except for both *Rhinolophus*), the percentage of weighted activity occurring before 20 % of the night had elapsed was weaker in summer than in other periods (mean difference of weighted activity between summer and spring: -7.7%, between summer and autumn: -5.4%). The percentage of weighted activity occurring before 20 % of the night had elapsed was also greater in spring than in autumn for 13 species out of 20 (mean difference of weighted activity between spring and autumn: 2.3 %).

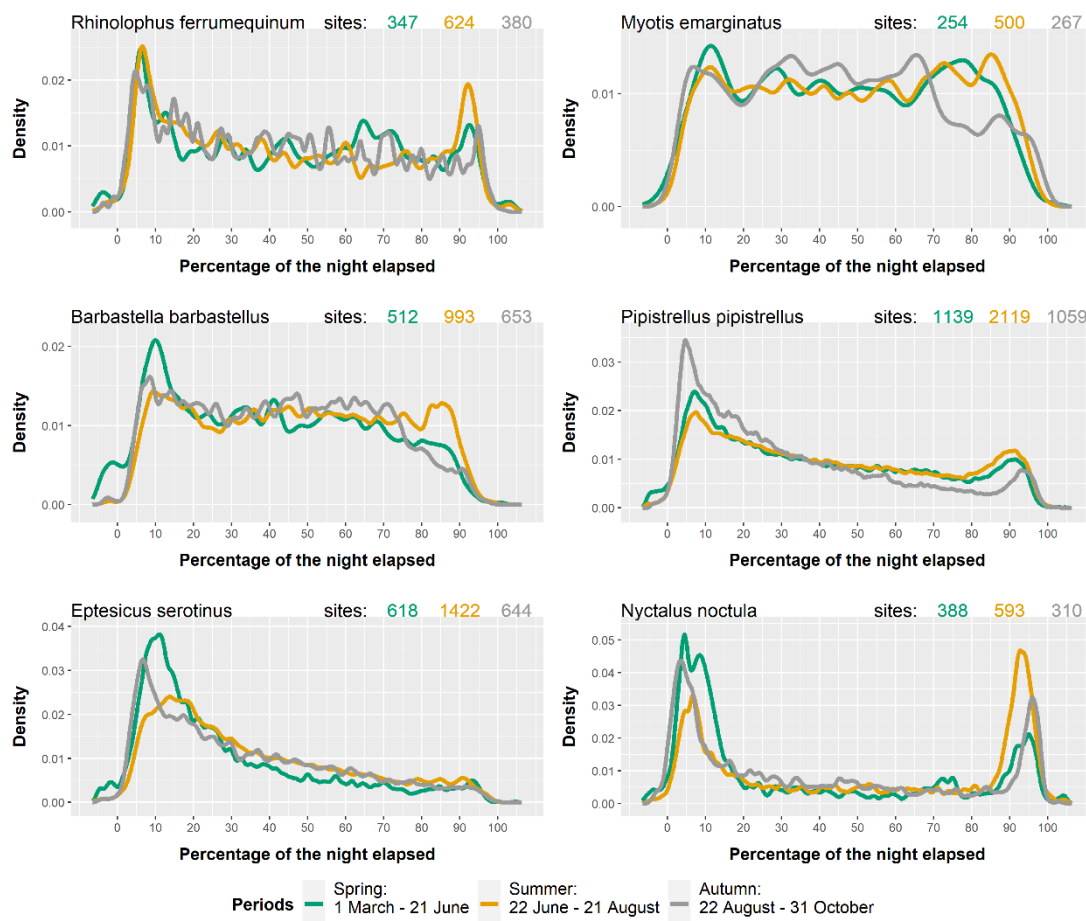


Figure 15: Activity distribution throughout the night for six species according to season, in percentage of the night elapsed. Top right, number of sites considered for each season.

4. Discussion

The use of a seven-year nationwide citizen science project gave us the opportunity to characterise the diel activity patterns of 20 insectivorous bat species at broad spatial and temporal scales. We showed that, although these patterns varied substantially between species, species could be grouped according to similarities in their temporal niches. Diel activity patterns also varied according to the season. We argue that this knowledge can be used to inform conservation measures to better preserve key times of bat diel activity.

4.1. Characterisation of diel activity patterns

We developed a methodology that can be applied to all taxa, whether abundant or rare, and at different spatial scales. This allowed us to go further than an hourly representation of bat passes by providing the times of key diel descriptors and a representation of activity distribution throughout the night, while accounting for the hierarchical structure of the dataset. The representativity and the large number of sites of the Vigie-Chiro dataset allowed to provide robust results that could be a first step towards further statistical analyses on the impacts of environmental (e.g. reproductive status, weather) and/or anthropogenic stressors (e.g. land-use change, pollution) on bat diel activity patterns while controlling for possible spatiotemporal autocorrelation issues (e.g. Mariton et al., 2022).

A strength of this study is to describe the diel activity patterns of many species using a single dataset, allowing direct comparisons between them. As diel activity patterns influence species' performance in a given environment, they can be considered as functional traits (Bennie et al., 2014) and we can thus distinguish functional groups based on similarities in their temporal niches. We distinguished: (1) “crepuscular” species with a marked bimodal activity starting shortly after sunset and ending shortly before sunrise, (2) “late” species with an overall well distributed activity throughout the night (i.e. no activity peak or a weak unimodal or bimodal activity pattern), starting late at night and ending earlier than the other species, (3) “intermediate” species with a unimodal or bimodal activity pattern and an overall activity that, while fairly early in the night, had intermediate start and end times compared to the other groups.

Such differences in the diel activity patterns of these functional groups can be explained by a trade-off between energetic needs and predation risks. Almost all the “crepuscular” and “intermediate” species are known to forage mainly on Diptera (Arthur and Lemaire, 2015; Jones and Rydell, 1994; Ware et al., 2020). It has been suggested that the unimodal to bimodal activity

pattern of these species, with peaks at dusk and dawn, resulted from the need to match the abundance peaks of this small insects (Dietz and Kalko, 2007; Jones and Rydell, 1994; Newson et al., 2015; Rydell et al., 1996; Swift, 1980). Almost all the species in these two groups are aerial edge- or open-foraging species that are usually considered to have a fast and agile flight, they are then less vulnerable to predation risks when exposed to light, allowing them to be active earlier than other species (Jones and Rydell, 1994; Voigt et al., 2021).

Conversely, most of the “late” species are gleaning or flutter-detecting narrow-foraging species that have a low and slow flight, making them more vulnerable to predation when exposed to light (Jones and Rydell, 1994; Voigt et al., 2021). The diet of the “late” species is composed of a large number of Lepidoptera (whose abundance remains quite high throughout the night) and/or flightless prey (Jones and Rydell, 1994; Ware et al., 2020). They can hence forage outside the dusk and dawn activity peaks of Diptera (Entwistle et al., 1996; Jones and Rydell, 1994; Marques et al., 2004; Rydell et al., 1996; Swift, 1997). Thus, it has been suggested that they can remain active throughout the night and avoid higher predation risks by emerging from their roost later than other species, when light levels are low (Entwistle et al., 1996; Jones and Rydell, 1994).

We observed variations in bat diel activity patterns according to the season. The overall patterns remained similar throughout the year, but the amplitude of the activity peaks varied. This is consistent with studies showing that the reproductive status of bats influences their diel activity pattern (Catto et al., 1995; Dietz and Kalko, 2007; Maier, 1992; Swift, 1997, 1980). We observed that there was a greater concentration of bat activity at the end of the night during early summer. The short duration of the night during early summer may force bats to exploit the whole night. Besides, early summer matches the lactation period of most species, during which energy requirements are the highest for reproductive females (Racey and Speakman, 1987) and during which they must return to the roost at night to suckle their young. Hence, a greater concentration of activity before sunrise could also be due to the need to forage longer and/or more efficiently (as some insects are abundant at dawn) to reach their high energy requirements while suckling their young after one or more activity bouts.

4.2. Diel activity patterns in conservation policies

We showed that bat diel activity patterns are highly variable according to the species, with variations between seasons. We advocate that this complexity be better accounted for in conservation policies aimed at reducing species' exposure to pressures. This would pave the

way for the design of conservation policies that would include both the spatial and the temporal distributions of species, for example, with stronger efforts to spare key diel times of species activity where conservation stakes are highest and to share time where human needs are highest. We illustrated below how conservation measures could better account for diel activity patterns through the example of two pre-existing but still developing measures focusing on pressures that have been recognised as potential drivers of changes in bat population: wind turbines and light pollution (Browning et al., 2021).

Part-night lighting (PNL) is increasingly implemented in Europe (Bennie et al., 2014). Only a few studies have focused on this mitigation measure against light pollution, however they agree on the need to encompass the range of activity of bats, by switching off streetlights earlier, for PNL to be efficient (Azam et al., 2015; Day et al., 2015; Hooker et al., 2022). Our method and results would allow for the possibility of defining a threshold based on a multi-taxa approach, including all bat species targeted by PNL. For instance, Azam et al. (2015) study was conducted in summer in a French regional park. They did not detect a significant effect of PNL on five out of the eight bat species studied, likely because the PNL scheme did not cover their key times of activity. According to our results, at this time and place, implementing a PNL scheme that would start before the mean time of the first pass of the “late” species (i.e. the group of species whose activity starts the latest and which is mainly composed of light-intolerant species) would result in switching off lights on average at 22:33, whereas at the studied sites streetlights were switched off around midnight.

Local people would probably object to the implementation of such a PNL scheme, as streetlights would be switched off when human needs for lighting are likely the highest (Gaston et al., 2012). Finding compromises between the light needs of humans and the dark needs of bats is therefore of importance, one solution being the consideration of both the spatial and the temporal distribution of bats. For instance, streetlights could be switched off early near key sites for bats (e.g. roosts, ecological corridors) while working on other mitigation measures – at least during key times for bat activity – where light is needed by humans and cannot be switched off as early as needed (e.g. changing the light spectrum, reducing light intensity and trespass or installing motion detectors).

Similarly, including bat diel activity patterns in algorithm-based curtailments of wind turbines would be of utmost interest (Behr et al., 2017; Friedenberg and Frick, 2021). This would allow the implement a stricter cut-in speed when fatality risks are susceptible to be the highest (e.g. dusk and dawn) than during the rest of the night. However, the curtailment algorithm of Behr et al. (2017), which is now the standard method for mitigating bat collision

risks of at wind farms in Germany, is one of the only algorithms we know of that consider bat diel activity patterns (Adams et al., 2021; Whitby et al., 2021). Adding an interaction between the time of the year and the time of the night could even increase the performance of such algorithms. For instance, in the dataset of Behr et al. (2017), *N. noctula* and *P. pipistrellus* were the species that accounted for most of the recordings. According to our results, the times of the two activity peaks of these species remain quite similar throughout the year but their amplitude change with, for instance, a proportionally greater activity at dawn in summer than during the rest of the year. These results hence raise the need for stronger curtailment efforts at dawn during summer.

4.3. Conclusions

We characterised the diel activity patterns of 20 bat species using a nationwide citizen science dataset. This new insight into the temporal ecology of bats can pave the way for fundamental analyses. For instance, insectivorous bat communities are diverse and probably highly structured by competition (Jachowski et al., 2014), studying how temporal niche partitioning determined their activity patterns would hence be of interest. From a conservation perspective, all mitigation measures aimed at reducing the impacts of stressors – whose intensity vary throughout the day – on biodiversity would benefit for a better consideration of species' diel activity patterns in addition to their spatial distribution. We strongly advocate multi-taxa approaches covering as many taxa known to be impacted as possible.

Data availability statement

The estimated densities of bat diel activity will be available on Zenodo open publication.

Bibliography

- Adams, E.M., Gulka, J., Williams, K.A., 2021. A review of the effectiveness of operational curtailment for reducing bat fatalities at terrestrial wind farms in North America. *PLoS ONE* 16, e0256382. <https://doi.org/10.1371/journal.pone.0256382>
- Arthur, L., Lemaire, M., 2015. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope ; Museum national d'Histoire Naturelle, Mèze; Paris.
- Aschoff, J., 1989. Temporal orientation: circadian clocks in animals and humans. *Animal Behaviour* 37, 881–896. [https://doi.org/10.1016/0003-3472\(89\)90132-2](https://doi.org/10.1016/0003-3472(89)90132-2)
- 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 Change Biol* 21, 4333–4341. <https://doi.org/10.1111/gcb.13036>
- Barataud, M., 2020. Acoustic ecology of European bats: species identification, study of their habitats and foraging behaviour, 2nd ed. ed, Inventaires & biodiversité series. Biotope Muséum national d'histoire naturelle, Mèze Paris.
- Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S.E., Julien, J.-F., Claireau, F., Kerbiriou, C., Bas, Y., 2019. Accounting for automated identification errors in acoustic surveys. *Methods Ecol Evol* 10, 1171–1188. <https://doi.org/10.1111/2041-210X.13198>
- 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>
- Behr, O., Brinkmann, R., Hochradel, K., Mages, J., Korner-Nievergelt, F., Niermann, I., Reich, M., Simon, R., Weber, N., Nagy, M., 2017. Mitigating Bat Mortality with Turbine-Specific Curtailment Algorithms: A Model Based Approach, in: Köppel, J. (Ed.), *Wind Energy and Wildlife Interactions*. Springer International Publishing, Cham, pp. 135–160. https://doi.org/10.1007/978-3-319-51272-3_8
- Bennie, J., Davies, T.W., Duffy, J.P., Inger, R., Gaston, K.J., 2014. Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Sci Rep* 4, 3789. <https://doi.org/10.1038/srep03789>
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)

- Browning, E., Barlow, K.E., Burns, F., Hawkins, C., Boughey, K.L., 2021. Drivers of European bat population change: a review reveals evidence gaps. *Mam Rev* mam.12239. <https://doi.org/10.1111/mam.12239>
- Bullock, D.J., Combes, B.A., Eales, L.A., Pritchard, J.S., 1987. Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrettus*). *Journal of Zoology* 211, 267–274. <https://doi.org/10.1111/j.1469-7998.1987.tb01533.x>
- Catto, C.M.C., Racey, P.A., Stephenson, P.J., 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology* 235, 635–644. <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>
- Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for bat conservation: Part-night lighting and bats. *Anim Conserv* 18, 512–516. <https://doi.org/10.1111/acv.12200>
- Dietz, M., Kalko, E.K.V., 2007. Reproduction affects flight activity in female and male Daubenton's bats, *Myotis daubentoni*. *Can. J. Zool.* 85, 653–664. <https://doi.org/10.1139/Z07-045>
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- Entwistle, A.C., Racey, P.A., Speakman, J.R., 1996. Habitat exploitation by a gleaning bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond. B* 351, 921–931. <https://doi.org/10.1098/rstb.1996.0085>
- 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
- Friedenberg, N.A., Frick, W.F., 2021. Assessing fatality minimization for hoary bats amid continued wind energy development. *Biological Conservation* 262, 109309. <https://doi.org/10.1016/j.biocon.2021.109309>
- Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. REVIEW: Reducing the ecological consequences of night-time light pollution: options and developments. *J Appl Ecol* 49, 1256–1266. <https://doi.org/10.1111/j.1365-2664.2012.02212.x>
- Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats. *Environmental Pollution* 307, 119552. <https://doi.org/10.1016/j.envpol.2022.119552>

- Husson, F., Josse, J., Pagès, J., 2010. Principal component methods-hierarchical clustering-partitional clustering: why would we need to choose for visualizing data? (Technical Report of the Applied Mathematics Department). Agrocampus.
- Husson, F., Lê, S., Pagès, J., 2009. Analyse de données avec R, 1st ed, Pratique de la statistique. Presses universitaires de Rennes, Rennes.
- Jachowski, D.S., Dobony, C.A., Coleman, L.S., Ford, W.M., Britzke, E.R., Rodrigue, J.L., 2014. Disease and community structure: white-nose syndrome alters spatial and temporal niche partitioning in sympatric bat species. *Diversity Distrib.* 20, 1002–1015. <https://doi.org/10.1111/ddi.12192>
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endang. Species. Res.* 8, 93–115. <https://doi.org/10.3354/esr00182>
- Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. B* 346, 445–455. <https://doi.org/10.1098/rstb.1994.0161>
- Laforge, A., Archaux, F., Coulon, A., Sirami, C., Froidevaux, J.S.P., Goux, N., Ladet, S., Martin, H., Barré, K., Roemer, C., Claireau, F., Kerbiriou, C., Barbaro, L., Algar, A., 2021. Landscape composition and life-history traits influence bat movement and space use: Analysis of 30 years of published telemetry data. *Global Ecol Biogeogr* geb.13397. <https://doi.org/10.1111/geb.13397>
- Lê, S., Josse, J., Husson, F., 2008. **FactoMineR** : An R Package for Multivariate Analysis. *J. Stat. Soft.* 25, 1–18. <https://doi.org/10.18637/jss.v025.i01>
- Lindenmayer, D., Hunter, M., 2010. Some Guiding Concepts for Conservation Biology. *Conservation Biology* 24, 1459–1468. <https://doi.org/10.1111/j.1523-1739.2010.01544.x>
- Maier, C., 1992. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *Journal of Zoology* 228, 69–80. <https://doi.org/10.1111/j.1469-7998.1992.tb04433.x>
- 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. *Environmental Pollution* 305, 119267. <https://doi.org/10.1016/j.envpol.2022.119267>

- Marques, J.T., Rainho, A., Carapuço, M., Oliveira, P., Palmeirim, J.M., 2004. Foraging Behaviour and Habitat use by the European Free-Tailed Bat *Tadarida teniotis*. *Acta Chiropterologica* 6, 99–110. <https://doi.org/10.3161/001.006.0108>
- Millon, L., Julien, J.-F., Julliard, R., Kerbiriou, C., 2015. Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecological Engineering* 75, 250–257. <https://doi.org/10.1016/j.ecoleng.2014.11.050>
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>
- Ochi, S., 2019. scorepeak: Peak Functions for Peak Detection in Univariate Time Series.
- R Core Team, 2022. R: A language and environment for statistical computing.
- Racey, P.A., Speakman, J.R., 1987. The energy costs of pregnancy and lactation in heterothermic bats. *Symp. zool. Soc. Lond.* 107–125.
- Robinson, M.F., Stebbings, R.E., 1997. Activity of the serotine bat, *Eptesicus serotinus*. *Myotis* 35, 5–16.
- Russo, D., Salinas-Ramos, V.B., Cistrone, L., Smeraldo, S., Bosso, L., Ancillotto, L., 2021. Do We Need to Use Bats as Bioindicators? *Biology* 10, 693. <https://doi.org/10.3390/biology10080693>
- Rydell, J., Entwistle, A.C., 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>
- Schoener, T.W., 1974. Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. *Science* 185, 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Sefick, S., 2016. Stream Metabolism-A package for calculating single station metabolism from diurnal Oxygen curves.
- Sutherland, W.J., Dicks, L.V., Petrovan, S.O., Smith, R.K. (Eds.), 2021. What Works in Conservation 2021. Open Book Publishers. <https://doi.org/10.11647/obp.0267>
- Swift, S.M., 1997. Roosting and foraging behaviour of Natterer's bats (*Myotis nattereri*) close to the northern border of their distribution. *Journal of Zoology* 242, 375–384. <https://doi.org/10.1111/j.1469-7998.1997.tb05809.x>

- Swift, S.M., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology* 190, 285–295. <https://doi.org/10.1111/j.1469-7998.1980.tb01428.x>
- van Klink, R., August, T., Bas, Y., Bodesheim, P., Bonn, A., Fossøy, F., Høye, T.T., Jongejans, E., Menz, M.H.M., Miraldo, A., Roslin, T., Roy, H.E., Ruczyński, I., Schigel, D., Schäffler, L., Sheard, J.K., Svenningsen, C., Tschan, G.F., Wäldchen, J., Zizka, V.M.A., Åström, J., Bowler, D.E., 2022. Emerging technologies revolutionise insect ecology and monitoring. *Trends in Ecology & Evolution* S0169534722001343. <https://doi.org/10.1016/j.tree.2022.06.001>
- Voigt, C.C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens, H.J.G.A., Mathews, F., Rydell, J., Spoelstra, K., Zagmajster, M., 2021. The Impact Of Light Pollution On Bats Varies According To Foraging Guild And Habitat Context. *BioScience* 71, 1103–1109. <https://doi.org/10.1093/biosci/biab087>
- Ware, R.L., Garrod, B., Macdonald, H., Allaby, R.G., 2020. Guano morphology has the potential to inform conservation strategies in British bats. *PLoS ONE* 15, e0230865. <https://doi.org/10.1371/journal.pone.0230865>
- Whitby, M.D., Schirmacher, M.R., Frick, W.F., 2021. The State of the Science on Operational Minimization to Reduce Bat Fatality at Wind Energy Facilities, A report submitted to the National Renewable Energy Laboratory. Bat Conservation International, Austin, Texas.
- Wolkovich, E.M., Cook, B.I., McLauchlan, K.K., Davies, T.J., 2014. Temporal ecology in the Anthropocene. *Ecol Lett* 17, 1365–1379. <https://doi.org/10.1111/ele.12353>

Appendices (*available in the Appendix I at the end of this PhD*)

Appendix A: Overview of scientific literature on bat diel activity patterns

Appendix B: Acquisition and curation of the biological data

Appendix C: Robustness of the automated identification

Appendix D: Additional information on the methods designed to characterise and compare bat diel activity patterns

Table E: Mean time of the key descriptors and time of the activity peaks in percentage of the night elapsed

Table F: Correspondence between species codes and Latin and English full names

Figure G: TLast, TPeakP2 and TMedianP2 for each bat species

Figure H: Activity distribution throughout the night for the twenty species studied

Table I: Descriptive metrics on bat activity distribution throughout the night

Appendix J: Clustering results

Figure K: Activity distribution throughout the night for the 20 species studied according to season

In short

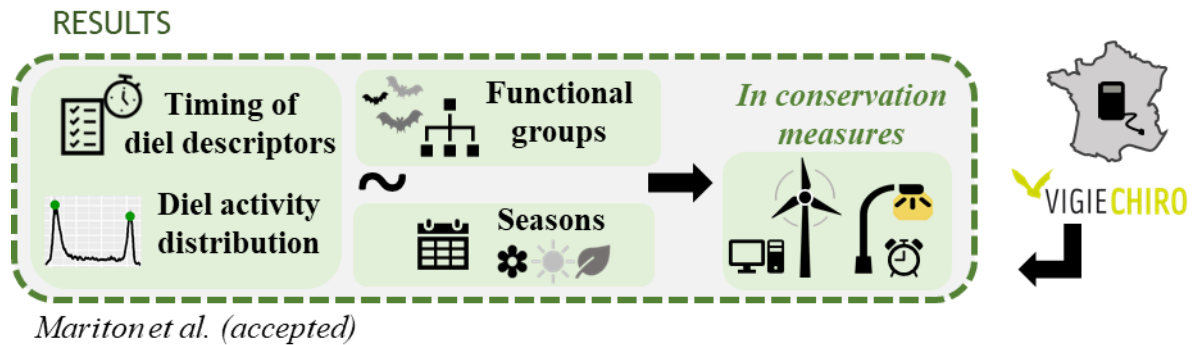


Figure 16: Results of Mariton et al. (accepted)

Main novelties:

- General knowledge on the temporal distribution of 20 European species, based on standardised and comparable metrics.
- Reproducible method to extract times of key descriptors and describe bat activity distribution throughout the night.
- Appeal to take diel activity rhythm into account in conservation measures and policies.

Result (Figure 16):

In this first chapter, we characterised the **diel activity pattern of 20 European bat species**. We designed a **method** based on the calculation of the timing of diel descriptors and an estimation of the diel activity distribution that can be applied not only to bat species but also to other taxa that can be monitored with passive acoustic devices. Furthermore, this method can be used for both common and rare species and at several scales. We showed that this characterisation allows to distinguish **functional groups of species**: “crepuscular” species (e.g. *P. pipistrellus* mean first recording was around 2.55 % of the night elapsed), “intermediate” (e.g. *E. serotinus* mean first recording was around 9.12 % of the night elapsed) and “late” species (e.g. *Plecotus austriacus* mean first recording was around 17.33 % of the night elapsed). Such functional groups can help design multi-taxa approaches for conservation. Although the overall diel activity patterns remained consistent throughout the year, we nevertheless found **seasonal variations** probably due to different energetic requirements according to bat reproduction status. We argue that accounting for these complex diel activity patterns would **help design efficient mitigation measures** (e.g. PNL schemes, wind turbine curtailment algorithms) to protect biodiversity from anthropogenic pressures.

Perspectives

In this study, we illustrated how, in theory, our characterisation of bat diel activity patterns could be included in measures such as PNL and wind turbine curtailment. We believe that this large-scale, synthesised study of bat temporal activity would be useful to conservation practitioners and policy makers.

Our results allow to estimate that in the French regional nature Park where Azam et al. (2015) conducted their study on PNL, light should be switched off much earlier (on average around 22:30 compared to midnight) to cover – at least – the range of activity of the “late” group of species (i.e. the functional group of species with the latest onset of activity and which is mainly composed of “light-intolerant” species). However, it has been suggested that local people would probably object to the implementation of such a PNL scheme, as streetlights would be switched off when human lighting needs are the highest (Gaston et al., 2012). We thus recommended to considering both bat temporal and spatial distributions in order to identify areas of high importance for bats (e.g. maternity roosts, key foraging areas or commuting corridors) where PNL could start early in the night and implement later PNL schemes coupled with other mitigations measures (e.g. lower light intensity) in other areas where lights are most needed for human activities and where the stakes for biodiversity are lower.

Furthermore, protecting all bat species from light pollution and not just those of the “late” group may be necessary (e.g. several species of the “crepuscular” and “intermediate” groups – such as *N. noctula*, *N. leisleri*, *P. pipistrellus* or *E. serotinus* – are considered as “vulnerable” or “near threatened” in France (UICN France et al., 2017)). Nevertheless, this would result in almost not switching on lights between sunset and sunrise (as, for instance, the mean time of the first pass for *P. pipistrellus* is 2.55 % of the night elapsed, which would be equivalent to 14 min after sunset for a nine-hour night).

However, it should be noted that species in the “crepuscular” and “intermediate” groups are mainly open- and edge-space-foraging species (i.e. species which are usually considered to be “light tolerant”) which are known to forage in the vicinity of streetlights (Rydell, 1992). For instance, Azam et al. (2015) showed that the activity of *P. pipistrellus*, *P. kuhlii*, *P. nathusii*, *N. leisleri* and *Nyctalus noctula* was higher in full-night and/or PNL sites compared to unlit ones. *P. pipistrellus* activity was even lower at PNL sites compared to full-night sites. One might therefore wonder whether we should try to protect these species from light pollution. To answer this concern, it is necessary to conduct studies at wider spatiotemporal scales in order to

Chapter I – Perspectives

evaluate the direct (e.g. alteration of landscape connectivity) and indirect (e.g. higher insects' mortality) impacts of ALAN on these species locally considered to be “light tolerant”.

Chapter 2: Impact of light pollution on bat diel activity patterns

“Au loin les lumières de la ville débordaient par trouées de la ligne des collines. Comme si l’urbain ne pouvait jamais nous laisser totalement en paix. Comme s’il fallait qu’il se signale à nous, menace autant que trésor, par son halo, par ses pierreries scintillantes.”

Alain Damasio, Les Furtifs

Based on the publication:

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. *Environmental Pollution* 305, 119267.

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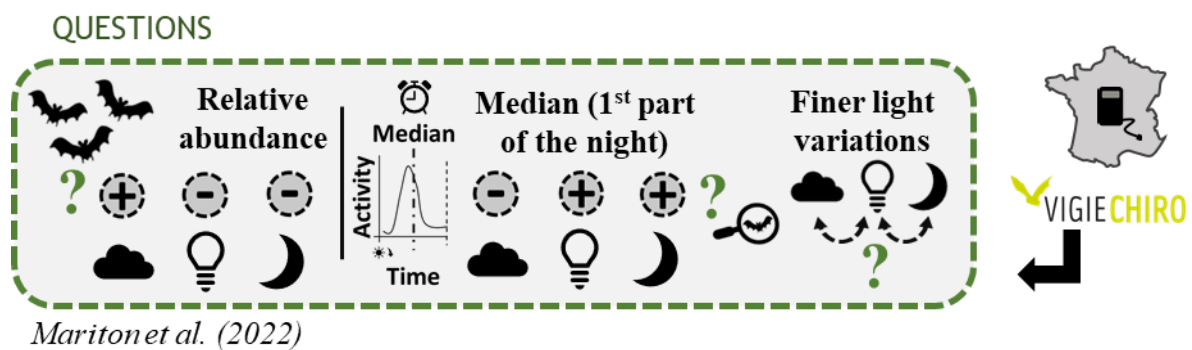


Figure 17: Questions of the second chapter

Context

At the local scale, it has been shown that open- and edge-space-foraging species (e.g. *Pipistrellus* spp., *Nyctalus* spp. and *Eptesicus* spp.), which are known to be “light tolerant”, are attracted to light sources where they exploit the predictable insect biomass (Azam et al., 2018; Rydell, 1992; Salinas-Ramos et al., 2021; Stone et al., 2015a; Zeale et al., 2018). The enhancing effect of ALAN on the activity of these “light tolerant” species has also been found at the landscape scale by Laforge et al. (2019) for *E. serotinus*, by Mathews et al. (2015) for *N. leisleri* and by Barré et al. (2021b) for *P. kuhlii* and *Pipistrellus pygmaeus*. ALAN might then appear to be beneficial for these species and attempting to protect them from it might seem irrelevant.

However, Laforge et al. (2019) and Barré et al. (2021b) also found that *Myotis daubentonii* and *P. pipistrellus* responded negatively to light pollution at the landscape scale, respectively. Similarly, Azam et al. (2016) found that the activity of *P. pipistrellus*, *P. kuhlii* and *E. serotinus* decreased when exposed to light pollution, at the city scale, Pauwels et al. (2019) found that *P. pipistrellus* activity was lower due to ALAN and Voigt et al. (2020) showed that the spatial use of *N. noctula* was largely limited by ALAN. Therefore, the responses of open- and edge-space-foraging species to light pollution appear to be more complex than might be expected by focusing only on the local scale. In particular, at the landscape scale, at least in some contexts, light pollution seems to be detrimental for these “light tolerant” species.

Several mechanisms could explain this lower abundance of open- and edge-space-foraging bats at large scales despite potential benefits at local scales: (1) ALAN may disrupt landscape connectivity for bats and thus affect their commuting behaviours (Hale et al., 2015; Laforge et al., 2019; Stone et al., 2009), (2) ALAN may contribute to the decline of insect populations and thus result in a decrease in the overall feeding biomass available for bats (Boyes et al., 2021; van Grunsven et al., 2020), (3) besides altering the spatial distribution of bats, ALAN may disrupt their temporal one. Indeed, all these mechanisms may lead to a lower individual fitness (e.g. due to higher mortality rates, lower reproductive success) and thus have potential cascading impacts on population dynamics.

As shown in the first chapter of this PhD, so far, studies on bat diel activity patterns are scattered and mainly conducted at local scales. It is thus not surprising that very few studies focused on the effect of anthropogenic pressures, such as ALAN, on the temporal distribution of bats. Nevertheless, some localised studies have shown that narrow-space-foraging species

(i.e. species considered to be “light-intolerant”) tend to emerge later from their roosts when exposed to light (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021), with potential cascading effects on reproductive success. In particular, Boldogh et al. (2007) found that the body mass of juveniles of *Myotis blythii* and *Myotis emarginatus* was lower in illuminated colonies than in non-illuminated colonies. They hypothesised that this might be due to a lower availability of insects for females in illuminated colonies. Indeed, delayed activity could result in an overall reduction in the time-budget for foraging and in a desynchronisation of bats with the peak of activity of their prey (Luo et al., 2021; Stone et al., 2015a), with potentially dramatic consequences for individual fitness and population dynamics.

However, to our knowledge, only two studies assessed the impact of light pollution on bat diel activity rhythm at commuting/foraging sites. Stone et al. (2009) showed in an experimental study that the onset of commuting behaviour in *Rhinolophus hipposideros* (a narrow-space-foraging species) was delayed by ALAN (8 sites) and Haddock et al. (2019) showed that the first recording of *Vespadelus vulturnus* (an edge-space-foraging species) was delayed in light-polluted sites (31 pairs of sites). Such studies are valuable, but they are rare, they focus on rather local scales and direct light pollution. Furthermore, there is a lack of studies on the potential impacts of light pollution on the timing of activity of the locally “light tolerant” open-foraging-space species.

Therefore, in this chapter, we first assessed the impact of direct and indirect light pollution, at the landscape scale, on the spatiotemporal distribution of an open-space-foraging species (*E. serotinus*) during gestation. This species has been shown to present a complex and contrasting responses to light pollution at different scales (see **Box 4** for details on the known consequences of ALAN on *E. serotinus*). It is therefore a particularly interesting species to explore the mechanisms explaining the responses of open-space-foraging bat species to ALAN. Using the data from the citizen-science program Vigie Chiro, we first intended to answer the following questions:

- (1) At the national scale, is the activity of a “light tolerant” species lower because of light pollution?**

The study of Laforge et al. (2019) was conducted in highly urbanised study sites, whereas the study of Azam et al. (2016) was based on acoustic surveys conducted at landscape scale in sites representative of the French land-cover. We could thus expect our results on *E.*

serotinus at the national scale to be similar to those of Azam et al. (2016), i.e. to find a decrease in the activity of *E. serotinus* in light-polluted landscapes. It should be noted that the study of Azam et al. (2016) was only conducted at the beginning of the night (approximately 1.5 h during the period of bat activity) and that also finding a decrease in *E. serotinus* activity due to ALAN would extend these results to the overall *E. serotinus* activity during the night.

(2) If so, does light pollution affect the diel activity pattern of this bat species at foraging sites and to what extent?

We hypothesised that even species usually considered to be “light tolerant” when foraging such as *E. serotinus* might delay their timing of activity in light-polluted landscapes.

By answering these questions, we hoped that this study would provide a better understanding of the sensitivity of bat species usually considered to be “light tolerant” to ALAN and could thus help inform public decisions on lighting reduction. Indeed, these species are mostly early-emerging species which would constraint PNL schemes to start very early or even not to switch on any light at all between sunset and sunrise. Where and when light cannot be switched off, other levers proposed in the literature to mitigate light pollution effect on biodiversity could be implemented, such as reducing light intensity. However, studies on the response of *E. serotinus* to light intensity show complex and not always consistent results (Azam et al., 2018; Lacoëuilhe et al., 2014) (**Box 4**). We thus intended to assess the following question:

(3) Can small variations in light levels have an impact on the spatiotemporal activity pattern of a light tolerant species? Such small variations can be due to natural light sources such as moonlight or to variation of the intensity of the skyglow because of cloud cover (Jechow et al., 2020, 2017; Kyba et al., 2011).



Box 4: Overview of the studies on the effects of light pollution on the Serotine bat (Eptesicus serotinus)

Local scale:

- Forage around/are attracted to streetlights (Robinson and Stebbings, 1997; Stone et al., 2015a)
- Positive effect of light intensity on activity (Lacoeuilhe et al., 2014)
- Activity peaking between 1 and 5 lx (Azam et al., 2018)
- No effect of streetlights (Pauwels et al., 2021; at 0 and 10 m: Azam et al., 2018)
- Negative effect of illuminance below 1 lx and over 5 lx (Azam et al., 2018)
- Negative effect of streetlights at 25 m and 50 m (Azam et al., 2018)
- Lower activity at PNL sites compared to unlit sites (Azam et al., 2015)

Landscape scale:

- Positive response to ALAN (Laforge et al., 2019)
- Negative effect of ALAN on activity (Azam et al., 2016)

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Even low light pollution levels affect the spatial distribution and timing of activity of a “light tolerant” bat species

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Highlights

Light pollution decreases bat abundance and delays their timing of activity.

Even low light levels affect bat abundance and timing of activity.

Skyglow enhanced by cloud cover increases light impact on the timing of activity.

Light pollution can even affect “light tolerant” open-space-foraging bat species.

Reducing direct and indirect light pollution at landscape scale is an urgent need.

Abstract (Figure 18)

By disrupting nocturnal landscapes worldwide, light pollution caused by Artificial Light At Night (ALAN) is recognised as a major threat to biodiversity. As even low light intensities might affect some taxa, concerns are arising about biological responses to widespread low light levels. We used data from a French citizen science bat monitoring program (1,894 full-nights monitored on 1,055 sites) to explore the landscape-scale effects of light on an open-space-foraging bat species, the Serotine bat (*Eptesicus serotinus*). We assessed this species' abundance and timing of night-time activity (median time of activity) at foraging sites. ALAN, and to a lesser extent moonlight, reduced *E. serotinus* abundance. ALAN delayed activity, and this delay was amplified during overcast nights. On the contrary, where there was no ALAN, the higher the cloud cover, the earlier the activity occurred. Cloud cover likely darkened the night sky in rural locations, whereas it amplified skyglow in light-polluted places, increasing ALAN effects on bats. Interestingly, moonlight also delayed activity but this effect was weakened where there was ALAN. Our study shows that even fine variations of light levels could affect the spatiotemporal distribution of a common species usually considered to be “light tolerant”, with potential cascading effects on individual fitness and population dynamics. It stresses how urgent it is to preserve and restore dark areas to protect biodiversity from light pollution while working on light intensity and directivity where ALAN is needed.

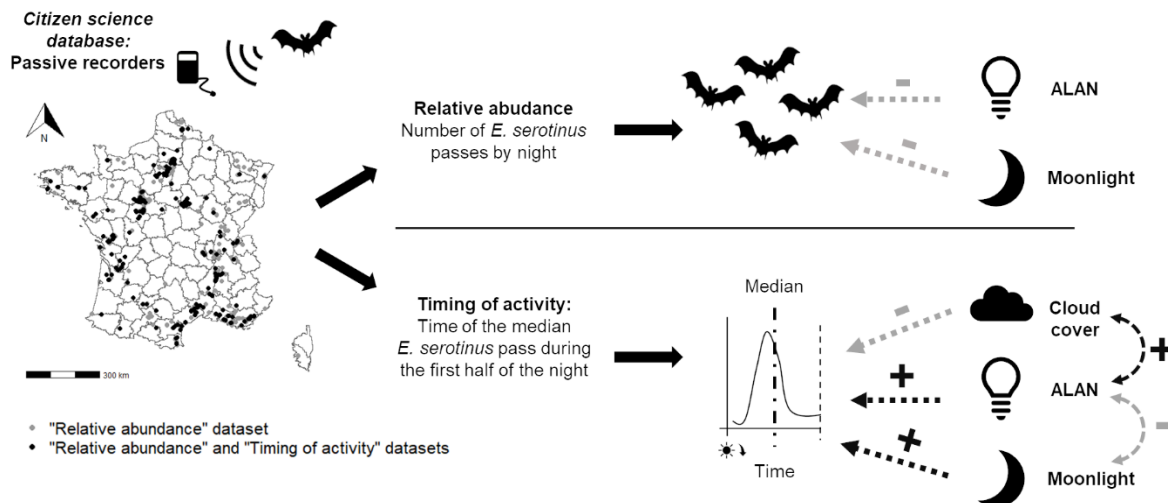


Figure 18: Graphical abstract of Mariton et al. (2022)

Keywords: Artificial Light At Night, Bat, Citizen science, Moonlight, Timing of activity, Skyglow

1. Introduction

Given forecasts predicting that, by 2030, global urban land cover will increase by 1.2 million km² (Seto et al., 2012), there are urgent needs to understand mechanisms underlying urbanisation effects on biodiversity (McKinney, 2002). In addition to leading to an increase in impervious surfaces, threatening biodiversity hotspots (Seto et al., 2012), it also results in the emissions of stressors such as noise, chemicals, and artificial light (Isaksson, 2015).

Artificial Light At Night (ALAN) and the resulting light pollution spreading even far from urban areas affect 23% of the globe's surface (Falchi et al., 2016), with a rate of 2.2% of areas being newly artificially lit per year (Kyba et al., 2017). As it accounts for 16.5% of global electricity demands (Zissis et al., 2021), it is an energetic use issue, but ALAN impacts on biodiversity are also a growing concern (Hölker et al., 2010; Koen et al., 2018; Longcore & Rich, 2004).

Light pollution has been shown to impact both nocturnal and diurnal species with potential dramatic effects on individual fitness, reproduction success and ecosystem functioning (Gaston et al., 2013; Owens et al., 2019; Svechkina et al., 2020). Many studies have focused on ALAN alteration of the species' movements and spatial distributions through attraction/repulsion behaviours (Longcore & Rich, 2004; Stone et al., 2015). However, ALAN also impacts the species' temporal distribution by changing natural light regimes, inducing shifts in the timing of activity of many taxa. For instance, it might disrupt the timing of activity of nocturnal taxa (e.g., arthropods: Lynn et al., 2021; amphibians: Secondi et al., 2021; mammals: Rotics et al., 2011), expand the timing of activity of diurnal taxa through the night and disrupt their sleep (e.g., birds: Alaasam et al., 2021; Amichai & Kronfeld-Schor, 2019; Raap et al., 2015), change timings of activity by inducing photoperiod-dependent behaviours outside of usual periods (e.g., birds: Kempenaers et al., 2010; mammals: Le Tallec et al., 2015). Overall, the cumulative effects of ALAN on the species' behaviour and community ecology have been recognized as a threat to ecosystem functions (Gaston et al., 2013; Longcore & Rich, 2004).

Developing lighting strategies to mitigate ALAN impacts on biodiversity is therefore essential (Hölker et al., 2010; Pauwels et al., 2021). Changing lighting intensity has been suggested as a possible measure (Gaston et al., 2012). However, a few studies suggest that dim light pollution levels, similar or lower to the full moonlight illuminance under clear skies (i.e. c. 0.1 – 0.3 lx), might impact biodiversity (Azam et al., 2018; Dominoni et al., 2013; Evans et al., 2007; Secondi et al., 2021).

Biological effects of widespread low light levels, induced for instance by skyglow (i.e. the artificial light scattered by atmospheric constituents and reflected back towards the Earth (Gaston et al., 2015; Kyba et al., 2017)), are an emerging concern (Gaston et al., 2013). Cloud cover has been shown to enhance this indirect light pollution by amplifying and expanding it to remote areas which are not affected by light pollution on clear nights (Jechow et al., 2017, 2020; Kyba et al., 2015). However, skyglow, and more generally, diffuse light pollution effects on biodiversity have been scarcely studied (Kupprat et al., 2020; Torres et al., 2020; Wilson et al., 2021).

As they are nocturnal, and directly exposed to light pollution, bats provide a useful system to study the impacts of ALAN on biodiversity. Natural pattern of light and dark is an important environmental cue synchronizing bat circadian rhythm (Erkert, 1982). The evening emergence of bats has been shown to be influenced by the sunset time (Erkert, 1982) while moonlight appears to influence the activity of some bat species (Saldaña-Vázquez & Munguía-Rosas, 2013). A perception of higher predation risks has been suggested as a driver of bat responses to light (Jones & Rydell, 1994; Rydell et al., 1996). Hence light pollution, by disrupting natural light regimes, hiding environmental cues and potentially increasing predation risks, might have dramatic effects on both bat abundance and timing of activity.

It has been shown that bat responses to ALAN depend on their foraging strategies and flight techniques (Jones & Rydell, 1994). Narrow-space-foraging bat species (mainly short-range-echolocators that slowly fly in confined spaces (Denzinger & Schnitzler, 2013; Voigt et al., 2021)) are considered to be light-intolerant at all spatial scales (Lacoeuilhe et al., 2014; Rydell, 1992; Salinas-Ramos et al., 2021; Spoelstra et al., 2017; Voigt et al., 2021; Zeale et al., 2018), whereas the responses of edge- and open-space-foraging species (mainly mid- and long-range-echolocators that fly faster than narrow-space-foraging species (Denzinger & Schnitzler, 2013; Voigt et al., 2021)) to light pollution are more complex and depend on the spatial scale considered (Pauwels et al., 2021; Voigt et al., 2021).

At local scale, edge- and open-space-foraging species, such as *Pipistrellus spp.* and *Eptesicus spp.*, tend to be attracted by light sources (Azam et al., 2018; Rydell, 1992; Salinas-Ramos et al., 2021; Stone et al., 2015; Zeale et al., 2018) probably because of the predictable foraging opportunities they offer by attracting high insect densities (Owens et al., 2019; Russo et al., 2019). However, at a slightly higher scale, Azam et al. (2018) showed that Serotine bats (*Eptesicus serotinus*, Schreber, 1774) experienced an avoidance behaviour from 25 to 50 m from streetlights probably because of a perception of higher predation risks. Few studies focus on ALAN effects on bats at landscape scale and they are not consensual regarding the responses

of open-space-foraging species. Laforge et al. (2019) found that, at landscape scale, *E. serotinus* responded positively to ALAN, and Mathews et al. (2015) found that the Lesser noctule (*Nyctalus leisleri*, Kuhl, 1817) was more frequent in light-polluted environments. Conversely, Azam et al. (2016) showed that, at landscape scale, *E. serotinus* abundance decreased because of light pollution and Voigt et al. (2020) showed that the spatial use of the Common noctule (*Nyctalus noctula*, Schreber, 1774) was largely constrained by ALAN. Hence, bat responses to ALAN may be driven by different mechanisms according to the considered spatial scales.

Several mechanisms might explain ALAN-mediated declines in bat abundance at landscape scale: (1) ALAN could disrupt bat commuting behaviours by decreasing landscape connectivity (Hale et al., 2015; Laforge et al., 2019; Stone et al., 2009; Voigt et al., 2020), (2) ALAN may interfere with insect development, reproductive success, movement behaviours and foraging behaviours (Boyes et al., 2020; Owens et al., 2019), it could therefore contribute the decline of insect populations (at local scale: Boyes et al., 2021; van Grunsven et al., 2020, possibly at global scale: Owens et al., 2019) and deplete landscapes of feeding resources for bats, (3) ALAN may disrupt the timing of bat nocturnal activity with potential cascading effects on their fitness and reproductive success, leading to potential population declines (Stone et al., 2015).

Roost illumination has been shown to delay the emergence of narrow-space-foraging bat species (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021). Some localised studies also suggest that the timing of bat activity might be disrupted at foraging sites due to ALAN. Haddock et al. (2019) highlighted that the first recording of Little forest bats (*Vespertilio vulturnus*, Thomas 1914, edge-space foraging) was delayed because of light pollution at forest edges and Stone et al., (2009) showed that the onset of commuting behaviour of the Lesser horseshoe bat (*Rhinolophus hipposideros*, Borkhausen, 1797, narrow-space-foraging species) was delayed by ALAN. Such shifts in the timing of activity – observed at foraging sites – might result in a desynchronization of bats with the peak of activity of their prey, a reduced time-budget to forage (Luo et al., 2021; Stone et al., 2015), and eventually it might impact their fitness and reproduction success. However, such studies are scarce, they focus on local scale and direct light pollution. Furthermore, there is a lack of studies on potential impacts of light pollution on the timing of activity of open-foraging-space species.

Intensity is an important factor to consider when studying bat responses to light pollution (Hale et al., 2015; Kerbiriou et al., 2020; Stone et al., 2015). Some studies even suggest that bat spatiotemporal distribution might be disrupted by slight modifications of light levels such as those due to moonlight (Appel et al., 2017; Gomes et al., 2020; Kolkert et al., 2020). However, this moonlight effect has not been much studied in temperate regions and is still discussed

(Saldaña-Vázquez & Munguía-Rosas, 2013). Because the skyglow maintains low light pollution levels in previously dark areas far from urban centres, it is crucial to determine if low intensities might disrupt bat spatiotemporal distribution.

In this study, we used the data from a national citizen science program to assess if light pollution, including at low intensities, affects the abundance and timing of activity of open-space-foraging bat species at their foraging sites, at landscape scale. We chose to focus on *E. serotinus*, an open-space-foraging bat species which is common in France but declining (Bas et al., 2020). Because their responses to light pollution are known to be complex and scale dependent (Azam et al., 2016, 2018; Stone et al., 2015), it is a particularly interesting species to explore the mechanisms explaining the responses of open-space-foraging bat species to ALAN. We predicted (1) that *E. serotinus* abundance would decrease with light intensities at foraging sites, (2) that their timing of activity at their foraging sites would be delayed later in the night because of light pollution, (3) that moonlight and cloud cover, by modifying light intensity, would also affect *E. serotinus* abundance and timing of activity.

2. Materials and methods

2.1. Bat surveys

2.1.1. Vigie-Chiro program

We used data from the “stationary points protocol” of the French citizen science bat monitoring program Vigie-Chiro (<https://www.vigienature.fr/fr/chauges-souris>), which has been coordinated by the French National Museum of Natural History since 2014. This standardised passive acoustic monitoring-based protocol encouraged volunteers to set ultrasonic recorders on hypothetical bat foraging sites for at least one full-night. To limit heterogeneity between devices, all recorders were configured with recommended settings.

2.1.2. Species identification

Species identification was made with the Tadarida software which automatically detects and extracts sound parameters of recorded sound events and classifies them into classes according to a confidence index value using a random forest algorithm (<https://github.com/YvesBas/Tadarida-C/>; Bas et al., 2017). Tadarida-D was used with default settings. Tadarida-C was used through consecutively Ta_Tc.R and ContextualClassif.R with default settings and R 3.2.3 (R Core Team, 2015).

We considered bat passes, defined as the occurrence of a single or several bat calls during a 5-s interval (Kerbiriou et al., 2019a; Millon et al., 2015). This metric had already been used in many studies (Azam et al., 2015; Barré et al., 2019; Millon et al., 2015; Pauwels et al., 2019), and, as 5 s is the mean call duration recorded for *E. serotinus* in France (Kerbiriou et al., 2019b), it was the best compromise between the risk of counting several times the same individual and the risk of missing another individual.

As automated identification can generate significant error rates, we chose to follow Barré et al., (2019) approach to ensure result robustness against automated identification errors. We considered *E. serotinus* passes with a maximum error rate tolerance of 0.5 to minimize false positives while keeping a high number of *E. serotinus* passes. Then, in order to ensure result robustness, we confirmed our results using a maximum error rate tolerance of 0.1 in Supplementary material A. Such a rate permitted us to limit false positives but discarded more true positives.

2.1.3. Spatiotemporal restrictions

We excluded surveys that might have been carried out near bat roosts, as we expected relative abundance to be higher there and driven by other factors than at foraging sites. There, we also expected an earlier timing of activity driven by specific events such as emergence. We also excluded surveys carried out in mountain environments (defined as sites above 500 m above sea level) to restrict our dataset to *E. serotinus* distribution range (Arthur & Lemaire, 2015) and to avoid any bias due to mountain environments (e.g., shades, specific climate) or to bat specific behaviours in these kind of environments (Cryan et al., 2000; McCain, 2007).

It had been shown by Catto et al. (1995) that while the timing of *E. serotinus* activity was unimodal to bimodal during gestation, it became more complex and multimodal during lactation. Therefore, we restricted our study to the gestation period of *E. serotinus* (from May 1st to 21st June (Catto et al., 1995; Harbusch & Racey, 2006)) because we expected that the timing of *E. serotinus* activity would be consistent during this period. Moreover, during gestation, female bats experience a greater wing loading that might affect their flight performance and make them more likely to be vulnerable to predation (Duvergé et al., 2000). Therefore, bats are likely to be prone to suffer from light pollution during this period. Finally, during this period, controlling for the potential confounding effect of night length is easier, as it is only decreasing.

2.2. Biological and environmental metrics

2.2.1. Abundance

We used the number of *E. serotinus* passes (named hereinafter “relative abundance”) during the night (from 30 min before sunset to 30 min after sunrise) as a proxy for abundance. As a matter of fact, because the number of feeding buzzes (i.e., call sequences produced by bats prior to a successful, or attempted, prey capture (Griffin & Lindsay, 1959)) has been shown to be strongly related to the overall number of bat passes, relative abundance can be used as reliable estimator of foraging activity (Put et al., 2019; Russo & Jones, 2003; Salvarina et al., 2018). Furthermore, commuting and foraging are not fully distinct activities for *E. serotinus* (Catto et al., 1996).

Our “relative abundance” dataset was made up of 21,452 *E. serotinus* passes, across 1894 full nights, on 1055 sites, from 2014 to 2020 (**Figure 19**). As *E. serotinus* can be found across the whole French territory (except in mountain areas that we discarded from our datasets) and, as this species is highly flexible when choosing their foraging habitats (Arthur & Lemaire, 2015), we hypothesised that all our survey sites were inside the range/habitat requirements of *E. serotinus*. We hence kept for our analyses the nights with no *E. serotinus* pass.

2.2.2. Timing of activity

As we postulated that no metric would be robust enough with less than 10 *E. serotinus* passes by night, we only kept nights with at least 10 passes during the whole night. We confirmed

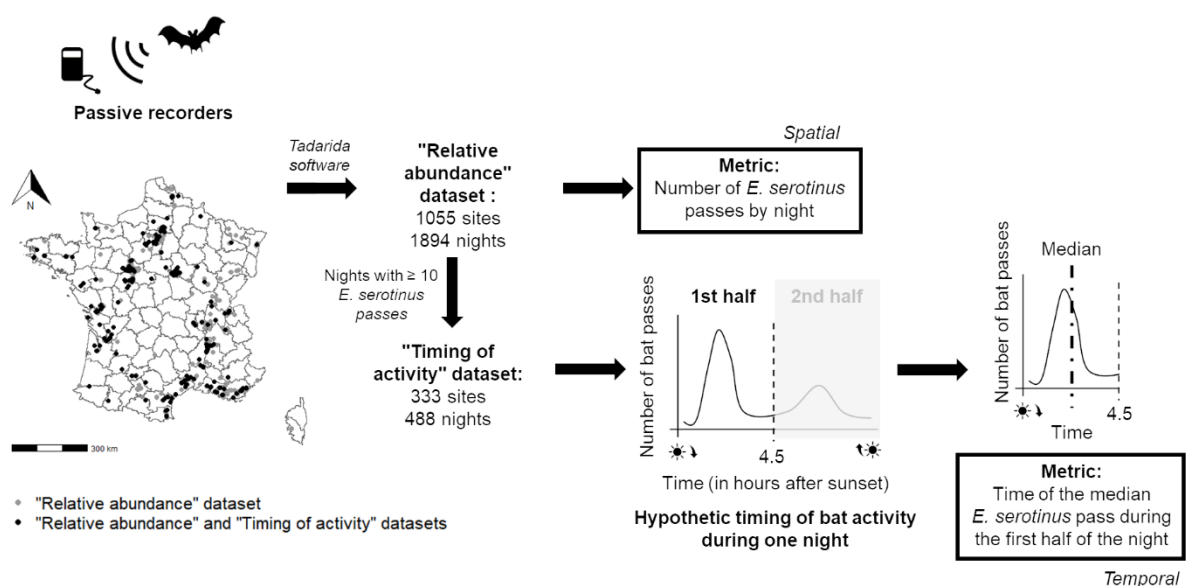


Figure 19: Data processing and construction of the biological metrics.

the pertinence of such a threshold according to the metric chosen to study the timing of activity by resampling the *E. serotinus* passes of the 100 nights with the most passes of our dataset (Supplementary material B). Among the 1894 full nights of the “relative abundance” dataset, 488 had at least 10 *E. serotinus* passes and they covered 333 sites. These nights constituted our “timing of activity” dataset (**Figure 19**).

Catto et al. (1995) showed that the timing of *E. serotinus* activity was unimodal to bimodal during pregnancy with a high peak after sunset and, possibly, a lower one before sunrise. We thus chose to focus only on the first part of the night (from 30 min before sunset to 4 h and 30 min after sunset) as it covered the first and higher peak of activity observed during gestation. The 488 first parts of night had 19,489 *E. serotinus* passes. The time of the first bat call recorded has been used in studies focusing on timings of bat activity at foraging sites (Haddock et al., 2019; Stone et al., 2009). However, in studies on bat emergence from roost, the median is preferred, even if it requires to monitor bats over a longer period (Bullock et al., 1987). It is less vulnerable to extreme values, as it does not rely on a single event and does not only reflect the onset of bat activity, but also its spreading across time. Therefore, to characterise the timing of activity, we chose to calculate the time of the median *E. serotinus* pass during the first 4 h and 30 min of the night, in seconds after sunset.

2.2.3. ALAN

To characterise light pollution around sites, we used radiance data (in $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$, excluding lunar contamination and cloud cover degradation) from the average radiance composite raster produced by the Earth Observation Group (EOG) using night-time data from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (EOG, Annual VNL V1 2016, <https://eogdata.mines.edu/products/vnl/>, Elvidge et al., 2017).

We hypothesised that *E. serotinus* spatiotemporal distribution at foraging sites would be influenced by the presence of light pollution across their whole vital domain at landscape scale (e.g., ALAN might delay their emergence from roosts and delay their arrival at foraging sites because of the barrier effect, or even result in lower feeding resources at the landscape scale). Therefore, we considered buffer zones with a 3000 m radius around the studied sites, as it covered the mean distance between foraging sites and roosts (Catto et al., 1996; Kervyn, 2001; Robinson & Stebbings, 1997). We ensured that the radiance gradient of our datasets was representative of the French radiance gradient (Supplementary material C).

To ensure the robustness of our approach, we re-analysed our datasets with the radiance value at the recorder sites rather than the mean value in 3000 buffer zones around sites (Supplementary material D).

2.2.4. Other factors affecting light levels

We considered other meteorological and astronomical factors that might influence light levels: (1) cloud cover (extracted from the NCEP/NCAR Reanalysis dataset, Kalnay et al., 1996) and (2) moonlight (we computed a variable that synthesised moon illumination values and moonrise hours (Supplementary material E)). We confirmed that the gradients of cloud cover and moonlight were wide enough to ensure robust analyses (respectively Supplementary materials F and G).

2.2.5. Weather

Temperature, precipitations and windspeed are known to influence bat spatiotemporal distributions, including *E. serotinus* one (Catto et al., 1996; Vaughan et al., 1997; Verboom & Huitema, 1997). As the timing of *E. serotinus* activity might be influenced not only by the weather conditions of the night but also by those of previous ones (Catto, Racey, et Stephenson 1995), we considered the daily weather and the difference with previous days.

Absolute measures of temperature may be misleading if *E. serotinus* populations adapt to local climatic conditions: a given temperature may represent a mild day for one population but a cold day for another. We therefore analysed temperature as anomalies relative to long-term (1980-2010) averages for each site.

Eventually, because of correlation issues, we did not include the precipitations of the day and the difference between the windspeed of the day and the windspeed of the previous days (further details on the calculation and selection of the weather variables are given in Supplementary material E).

2.2.6. Land-use

The higher the landscape quality for bats, the greater the relative abundance will be, and the less bats may have to commute to arrive at their foraging sites. We chose to calculate seven environmental variables known to influence the spatiotemporal distribution of bats, especially *E. serotinus*, in 3000 m buffer zones around sites: proportions of deciduous forest, conifer forest, grasslands and artificialized surfaces (dense and diffuse impervious surfaces, industrial and commercial estates), habitat diversity (Shannon's diversity index), density of small woody

features, minimum distance from freshwater. The buffer zones around the sites of our datasets covered the same land-use type gradient as buffer zones around sites randomly selected in France. Correlation issues led us not to include road density and proportion of crops despite their potential effects on the spatiotemporal distribution of bats (Supplementary material E).

ALAN and artificialized surfaces were highly correlated (Pearson correlation coefficient equal to 0.88 for the “relative abundance” dataset and 0.83 for the “timing of activity” dataset). However, as this study aimed at assessing if ALAN by itself might impact *E. serotinus* spatiotemporal distribution, we had to consider these two variables. Thus, we chose to adapt our statistical modelling methods (see below) to consider both artificialized surfaces and ALAN despite their correlation.

2.3. Statistical analyses

2.3.1. Full models

We used Generalized linear mixed models (GLMM) to test the influence of light level on the biological metrics (R 4.0.4 (R Core Team, 2021), R package *glmmTMB*). We used a negative binomial distribution with a quadratic parameterization for “relative abundance” analyses and a gaussian distribution for “timing of activity” analyses.

We included all variables previously described in our models as fixed effects along with Julian day and its quadratic effect to control any potential effect of the night length or of the gestation progress. For “relative abundance” analyses, we added the recorder type used as a fixed effect, to control the different performances of recorders in detecting bats. All quantitative fixed effects were scaled, so that the regression coefficients calculated would be comparable in their effects and magnitudes (Schielzeth, 2010).

We tested several interactions that could affect light levels: interaction (1) between cloud cover and ALAN as cloud cover might amplify light pollution (Jechow et al., 2017; Kyba et al., 2015), (2) between moonlight and ALAN as, for instance, light pollution could be so strong that moonlight does not have an effect on bats anymore, (3) between moonlight and cloud cover as the latter could conceal the moon. Note that we also added an interaction between temperature anomaly of the day and difference with temperature anomalies of the previous days because bat responses to temperature extremes may depend upon whether previous days have also been too hot or cold to forage effectively.

Our dataset had a spatiotemporal structure: (1) a site might have been monitored several nights, (2) if these nights were consecutive, they formed a single “participation” (i.e., a single monitoring session during which the same recorder stayed at the same place during at least one full night to several in a row); if they were not consecutive, they formed several “participations”. Thus, we included a random effect on participations nested on sites for “relative abundance” analyses. For “timing of activity” analyses, the smaller dataset did not allow the use of such a random structure. As we already considered Julian day, we did not include the random effect on participation but we kept the random effect on sites.

We hypothesised that, the more *E. serotinus* passes there would be during the night, the more accurate the calculation of the metric used to characterise the timing of activity would be. We therefore put a weight on the logarithm of the number of *E. serotinus* passes during the first 4 h and 30 min after sunset for the analyses on the timing of activity.

The 3000 m buffer zones around some sites of our datasets overlapped, however, according to Zuckerberg et al. (2020), overlapping landscapes are not a violation of independence and they do not induce nor protect from spatial autocorrelation. There was some spatial autocorrelation for both the “relative abundance” and the “timing of activity” analyses. We added latitude as a fixed effect to correct it. As some spatial autocorrelation remained for the “timing of activity” analyses, we corrected it by adding an autocovariate computed with the autocov_dist function (R package *spdep*).

The full models were the following ones (all variables are summarized in Table H; model assumptions were checked according the procedure described in Supplementary material I):

$$\begin{aligned} \text{Metric} \sim & \text{ALAN} + \text{Conifer_forest} + \text{Deciduous_forest} + \text{Grasslands} + \text{Artificialized_surfaces} + \\ & \text{Habitat_diversity} + \text{Small_woody_features} + \text{Min_distance_freshwater} + \text{Temperature} + \\ & \text{Difference_temperature} + \text{Windspeed} + \text{Difference_precipitations} + \text{Cloud_cover} + \text{Moonlight} \quad \text{Eq. (1)} \\ & + \text{Julian_day} + \text{Julian_day}^2 + \text{Recorder_type}^* + \text{Temperature:Difference_temperature} + \\ & \text{Moonlight:Cloud_cover} + \text{Moonlight:ALAN} + \text{Cloud_cover : ALAN} + \text{Latitude} + \text{autocov}^{**} \\ & + (1 | \text{site/participation})^* + (1 | \text{site})^{**} \end{aligned}$$

With:

Metric: “relative abundance” or “timing of activity” metric

*: only for “relative abundance” analyses

**: only for “timing of activity” analyses

2.3.2. Model averaging

We chose the model averaging approach so that we could assess both the effects of artificialized surfaces and ALAN despite their correlation. The aim was to compare their relative importance on the relative abundance and timing of activity.

We processed all the models resulting from all the combinations of the fixed effects with this condition: never include artificialized surfaces and ALAN in the same combinations (i.e., never include these two variables in the same models) (R package *MuMIn* and *snow*). For “relative abundance” analyses, we always included latitude (to correct spatial autocorrelation) and recorder type (to control possible bias). For “timing of activity” analyses, we always included latitude and the autocovariate (to correct spatial autocorrelation). Then, a model averaging was computed within a $\Delta AICc$ (second order bias correction for Akaike Information Criterion) of six points (Burnham et al., 2011; Grueber et al., 2011; Richards, 2007). Since the inclusion of models with interaction terms involving ALAN might favour selection of ALAN over artificialized surfaces, we repeated all analyses excluding those terms and found similar results as those obtained with interaction terms (Supplementary material J).

To assess if the variables had an effect on the relative abundance or the timing of activity, we compared the relative importance of the variables (i.e., the sum of weights (SW)). However, as it has been shown that only considering this criterion is hazardous, we crossed it with the 95% confidence intervals of regression coefficients obtained with the model averaging (Galipaud et al., 2014). Hence, we considered that a variable had an effect when the confidence interval of its regression coefficient did not overlap zero and its SW was above 0.6.

We checked the robustness of our results by comparing them to those we would have obtained by only considering the best model and the significance of the estimates included in it, and we found concordant results. We also confirmed that not discarding complex versions of any other model with a lower AICc value (as suggested by Richards et al., (2011)), was not an issue in our analyses. Furthermore, to ensure that our results were sound against the multicollinearity issues raised by Cade, (2015), we also computed model averaging on standardised estimates based on partial standard deviations for their variables and found similar results as with a “classical” standardisation of estimates (see Supplementary material K for these additional analyses).

3. Results

3.1. Relative abundance

ALAN had a strong negative effect on relative abundance. It was the variable with the greatest effect size of all those tested (**Table 2**) (see Table L for details on the model averaging results) and its SW was much greater than the artificialized surfaces one. For an average mid-sized town (mean radiance $7.8 \text{ nW.sr}^{-1}.\text{cm}^{-2}$, Table M), there was 18% less *E. serotinus* passes than in a dark place (radiance = $0 \text{ nW.sr}^{-1}.\text{cm}^{-2}$; assuming all other variables held at mean levels).

When considering the ALAN value at the recorder sites rather than the mean ALAN value in the 3000 m buffer zones, the AICc of the best model was higher and artificialized surfaces had a greater SW than ALAN (Supplementary material D). The estimate (-0.014) and confidence interval (-0.020 ; -0.007) of ALAN when considering ALAN at the recorder sites were nonetheless similar to those obtained when considering the mean ALAN value in the 3000 m buffers zones (**Table 2**).

Moonlight also had a negative impact on relative abundance while there was no clear effect of cloud cover and interactions.

Besides variables reflecting light levels around sites, relative abundance increased with favourable meteorological conditions (high temperature, higher temperature than the previous days, less rain than the previous days), with Julian day and with habitats known to increase bat abundance (deciduous and conifer forests, habitat diversity and small woody features).

3.2. Timing of activity

Increased ALAN delayed the timing of activity, and this delay was increased by a higher cloud cover (**Table 2**, **Figure 20**, Figure N). For an average mid-sized town (mean radiance $7.8 \text{ nW.sr}^{-1}.\text{cm}^{-2}$, Table M), activity was delayed by 6 minutes on a clear night and by 10 minutes on a night with a 50% cloud cover, compared to a site with no ALAN (radiance = $0 \text{ nW.sr}^{-1}.\text{cm}^{-2}$; assuming all other variables held at mean levels). Where there was no ALAN, increased cloud cover provoked an earlier activity, whereas above an ALAN value of $31.04 \text{ nW.sr}^{-1}.\text{cm}^{-2}$, the cloud cover seemed to delay the timing of activity.

Table 2 : Model averaging results for a ΔAIC_c of six points for the “relative abundance” and “timing of activity” analyses: estimate, sum of weights (SW) and 95% confidence interval (CI) for each variable (apart from latitude and recorder type that were fixed for “relative abundance” analyses and latitude and the autocovariate that were fixed for “timing of activity” analyses) (estimates in bold when the 95% confidence interval did not overlap zero and the SW was above 0.60). All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable.

Variables	Relative abundance			Timing of activity		
	Estimates	SW	CI (95%)	Estimates	SW	CI (95%)
Temperature	0.010	1.00	0.005 ; 0.015	0.031	0.31	-0.047 ; 0.110
Difference_temperature	0.012	1.00	0.007 ; 0.016	0.114	1.00	0.064 ; 0.165
Windspeed	-0.002	0.47	-0.006 ; 0.001	-0.093	1.00	-0.136 ; -0.050
Difference_precipitations	-0.006	1.00	-0.010 ; -0.002	-0.053	0.91	-0.099 ; -0.006
Julian_Day	0.012	1.00	0.008 ; 0.017	-0.031	1.00	-0.119 ; 0.057
(Julian_Day) ²	-0.002	0.32	-0.007 ; 0.003	0.142	1.00	0.061 ; 0.223
Cloud_cover	0.003	0.67	-0.001 ; 0.006	-0.155	1.00	-0.199 ; -0.110
Artificialized_surfaces	-0.016	0.11	-0.023 ; -0.009	NA	NA	NA
Grassland	-0.005	0.50	-0.011 ; 0.002	0.012	0.18	-0.111 ; 0.135
Deciduous_forest	0.010	1.00	0.004 ; 0.015	-0.059	0.26	-0.189 ; 0.072
Conifer_forest	0.012	1.00	0.006 ; 0.019	-0.017	0.18	-0.138 ; 0.104
Habitat_diversity	0.007	0.82	0.000 ; 0.013	0.017	0.18	-0.090 ; 0.123
Min_distance_freshwater	-0.004	0.37	-0.012 ; 0.004	0.041	0.20	-0.107 ; 0.190
Small_woody_features	0.008	1.00	0.003 ; 0.014	-0.067	0.36	-0.181 ; 0.047
ALAN	-0.019	0.89	-0.027 ; -0.010	0.235	1.00	0.117 ; 0.354
Moonlight	-0.006	1.00	-0.010 ; -0.002	0.092	1.00	0.032 ; 0.152
Difference_temperature :Temperature	0.001	0.24	-0.003 ; 0.004	-0.024	0.09	-0.066 ; 0.019
Cloud_cover:Moonlight	0.002	0.21	-0.002 ; 0.005	-0.013	0.21	-0.055 ; 0.030
ALAN:Cloud_cover	-0.001	0.14	-0.006 ; 0.003	0.059	0.95	0.011 ; 0.106
Moonlight:ALAN	-0.001	0.19	-0.005 ; 0.004	-0.073	1.00	-0.120 ; -0.027

Moonlight also delayed the timing of activity. However, this effect was weakened by increasing ALAN (Table 2,

Figure 21, Figure O). Compared to a night with no moonlight (0%), a moonlight of 50% delayed activity by 4 minutes at the average mid-sized town, and by 9 minutes at a site with no ALAN (assuming all other variables held at mean levels). Above an ALAN value of $15.40 \text{ nW.sr}^{-1}.\text{cm}^{-2}$, the moonlight effect even seemed to shift the timing of activity earlier.

When considering the ALAN value at the recorder sites rather than the mean ALAN value in 3000 m buffer zones, the AICc of the best model was higher and these two interactions no longer had any significant effect (Supplementary material D).

The timing of activity was not affected by any of the land-use variables, in particular, artificialized surfaces were not included in any models of the model set. The timing of activity was delayed by favourable meteorological conditions (higher temperature than the previous days, less rain than the previous days, less wind) and varied according to Julian day (Julian day led to an earlier activity until approximatively the two-third of the period considered, then it delayed activity) (Table 2).

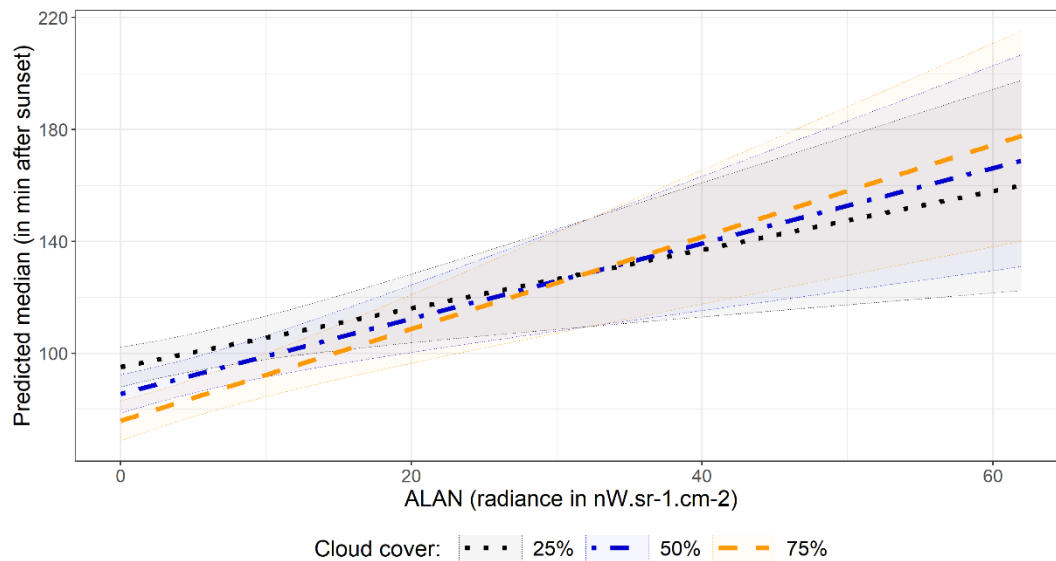


Figure 20 : Interaction between ALAN and cloud cover. Predicted values and 95% confidence intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they were previously scaled) apart from ALAN and cloud cover. This graph represents the median time of activity according to ALAN (radiance back transformed in $\text{nW.sr}^{-1}.\text{cm}^{-2}$) for three values of cloud cover (see to visualise the median time of activity according to cloud cover for three values of ALAN).

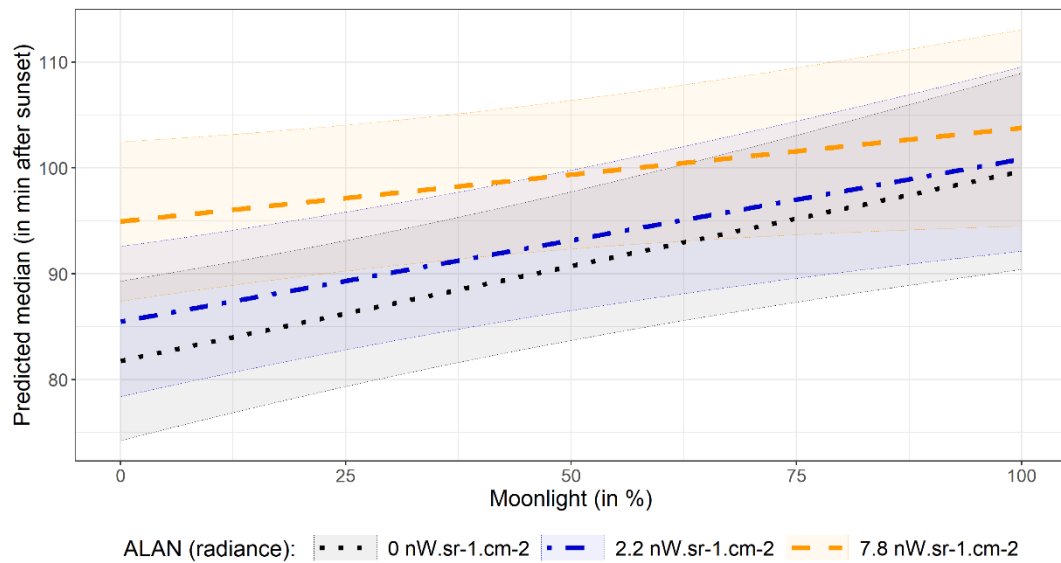


Figure 21 : Interaction between moonlight and ALAN. Predicted values and 95% confidence intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they were previously scaled) apart from moonlight and ALAN. This graph represents the median time of activity according to moonlight (back transformed in %) for three values of ALAN (2.2 nW.sr⁻¹.cm⁻² being the mean radiance of French municipalities of 1,000 to 5,000 inhabitants and 7.8 nW.sr⁻¹.cm⁻² being the mean radiance for municipalities of 5,000 to 10,000 inhabitants, see Table M) (see Figure O to visualise the median time of activity according to ALAN for three values of moonlight).

4. Discussion

This study is one of the first to test natural and artificial light effects on both the spatial and temporal distributions of an open-space-foraging bat species at their foraging sites, at landscape scale. Light pollution reduced *E. serotinus* relative abundance and delayed their timing of activity. The use of a seven-year citizen science database allowed us to consider a whole national territory and gave us the unique opportunity to show the impact of fine light intensity variations (moonlight, skyglow amplified by cloud cover) on *E. serotinus* spatiotemporal distribution.

4.1. Relative abundance

At landscape scale, ALAN was responsible for a decrease in *E. serotinus* relative abundance at their foraging sites. The obtained results when considering ALAN at local scale confirmed that this decrease in abundance was not the reflection of a localised avoidance behaviour. Such results are consistent with Azam et al. (2016) study results on open-space-foraging bat species. Using a different dataset from the Vigie-Chiro program (data from one-hour car surveys), they found that *E. serotinus* abundance was lower when exposed to light pollution at landscape scale. On the contrary, Laforge et al. (2019) found that *E. serotinus* had a positive response to light pollution at a city scale. The authors hypothesized that in their highly urbanized study sites, with few optimal foraging areas, streetlights might have become sub-optimal foraging areas; this could explain the difference between their own results and those obtained by Azam et al. (2016).

Furthermore, we found that even the low light levels created by moonlight reduced *E. serotinus* abundance. In South America, some authors found that moonlight affected bat abundance making it higher or lower depending on the species (Appel et al., 2017; Gomes et al., 2020; Vásquez et al., 2020). However, to our knowledge, this study is one of the first to show such an effect, called “lunar phobia”, on the abundance of a European open-space-foraging bat species. Ciechanowski et al., (2007) detected a decreasing abundance of Daubenton's bat (*Myotis daubentonii*, Kuhl 1817), an edge-space-foraging species, when exposed to moonlight but they did not detect any effect on *E. serotinus*. This result difference can be explained by the fact that they did not consider the hours of moonrise in their analyses. Furthermore, they began to record bats 30 min after sunset. If moonlight impacted the early activity, it might therefore not have been detected. Overall, the effect we found of moonlight on abundance indicates that even low, occasional or periodic increases of light levels could result in lower *E. serotinus* abundance.

The decrease of an open-space-foraging species abundance when exposed to light, despite potential positive impacts locally, could be explained by several mechanisms. In the short-term, light might impact bat abundance by modifying prey availability. For instance, insect abundance has been shown to vary according to moonlight (Bowden & Church, 1973; Williams & Singh, 1951) and Lang et al. (2006) linked White-throated round-eared bat (*Lophostoma silvicolium*, D'Orbigny, 1836) higher abundance during new moon compared to full moon periods to a higher activity of the katydids they prey on. Furthermore, a perception of increased predation risks when exposed to light has also been suggested as a potential driver

of bat responses to light (Jones & Rydell, 1994; Rydell et al., 1996). This may result in changes of the timing and duration of bat activity during bright nights to limit predation risks. In this context, the tolerance of open-space-foraging bat species to light pollution when foraging could only be the result of a local trade-off between their energetic needs and the risk of predation, the higher prey concentrations around light sources offsetting greater risks of being seen by predators.

When bright conditions are created by moonlight, bats may be able to compensate their lower activity during those bright nights by being more active during darker ones. But, when these bright conditions are due to ALAN, they are constant, and bats could then either not be able to reach their energetic needs in the long-term or be compelled to be active despite higher predation risks. It could result in lower individual fitness and dramatic disruptions of population dynamics.

Furthermore, in the medium- and long-terms, light pollution might not only impact bat fitness, but also the fitness of the insect they eat. Some authors suggested that ALAN may be a driver of insect population declines in light-polluted areas (Boyes et al., 2021; Grubisic et al., 2018; van Grunsven et al., 2020) or even globally (Owens et al., 2019). Therefore, light pollution may affect bat abundance by decreasing the overall available feeding resources at landscape scale.

Eventually, light pollution might not only disrupt bat foraging behaviours, but also their commuting ones. For instance, Hale et al. (2015) showed that *P. pipistrellus* movements were restricted in brightly lit gaps, ALAN creating a barrier effect impairing landscape connectivity. Bats may hence have to find longer routes to reach their foraging sites with potential greater energetic costs that can affect their individual fitness and, *in fine*, their abundance (Stone et al., 2009). If the energetic costs of alternative routes are too high, ALAN might even result in a reduction of the accessible lands to forage for bats at landscape scale.

Further research would be needed to determine if this decrease in abundance at landscape scale when exposed to ALAN results from a redistribution of *E. serotinus* populations in darker places at a wider scale and/or from lower individual fitness which might lead to population declines. In particular, it is worth noting that Bas et al. (2020) showed that *E. serotinus* population declined by -30% between 2006 and 2019 in France. It raises the question of the causes of such a strong decline and, what role light pollution could be playing.

4.2. *Timing of activity*

Increased ALAN delayed the timing of activity, and this delay was increased by higher cloud cover when considering ALAN at landscape scale. Firstly, the overall ALAN delaying effect we found is consistent with the few and localised studies focusing on edge- and narrow-space-foraging bat species at foraging sites (Haddock et al., 2019; Stone et al., 2009) which also showed that ALAN delayed the timing of activity, our study expanding it to open-space-foraging species at wide scale. Secondly, cloud cover amplifying the ALAN effect at landscape scale is consistent with studies showing that skyglow (i.e., diffuse light pollution glow at landscape scale, even affecting areas that are not directly lit (Kyba et al., 2017)) is amplified during overcast nights (Jechow et al., 2017; Kyba et al., 2015). By amplifying skyglow, cloud cover can thus increase the effects of ALAN on wildlife (van Hasselt et al., 2021). On the contrary, where there was no ALAN, cloud cover shifted the timing of activity earlier likely by darkening the night sky in rural locations (Jechow et al., 2016). Hence, dynamic and fine variations of light levels affect the timing of *E. serotinus* activity.

Interestingly, moonlight also delayed the timing of activity. However, this effect was weakened by increasing ALAN. Such results suggest that light pollution masks other luminous environmental cues. It also shows that even periodic or occasional increases of light levels could impact *E. serotinus* timing of activity.

The delayed timing of activity around light-polluted foraging sites could be explain by several hypotheses. First, bat emergence from roosts might be delayed because of ALAN, as shown by a few studies on narrow-space-foraging species (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021; McAney & Fairley, 1988). Also, as light pollution is known to decrease landscape connectivity for bats (Hale et al., 2015; Laforge et al., 2019; Stone et al., 2009), a delayed timing of activity at foraging sites could be the result of longer flights to reach them. Then, if bats arrive later, they might potentially suffer from a desynchronization with the peak of activity of their prey (Luo et al., 2021). It could result in a reduced efficient time-budget (i.e., a reduced period during which bats may feed on the prey their diets are mainly composed of) and/or in longer foraging durations to reach their energetic needs.

Delayed timing of activity could potentially lead to a reduced efficient time-budget to forage for bats and/or higher energetic costs to forage. If these delays are occasional, for instance because of brighter nights caused by moonlight, bats may be able to compensate potential harmful effects by taking advantage of darker nights to reach their energetic needs. However, as light pollution is a constant stressor, delays caused by ALAN may eventually prevent bats from reaching their energetic needs in the medium- and long-terms, which could

have cascading effects on individual fitness and population dynamics, and thus result in lower bat abundance at landscape scale when exposed to ALAN. For instance, Boldogh et al. (2007) showed that juveniles of narrow-space-foraging bat species were smaller in illuminated buildings, where bat emergence was delayed because of ALAN. However, our study only focuses on the gestation period and further investigations should be carried out for the lactation one – when energetic needs are even higher – to assess whether ALAN still has an effect on the timing of *E. serotinus* activity.

4.3. Management consequences

Abundant and widespread bats such as *E. serotinus* provide important ecosystem functions (Mathews et al., 2015). Tiede et al. (2020) showed that, among the most frequent taxa *E. serotinus* fed on, there were many potential pests of forestry and agriculture, this bat species therefore contributing to biological control. More generally, they suggested that *E. serotinus* contributes to the stabilization of food webs and ecosystems, by exploiting seasonally abundant insect prey. Hence, ALAN impacts on *E. serotinus* spatiotemporal distribution may have dramatic consequences on the ecosystem services they provide and might, more generally, have harmful effects on ecosystem functioning.

These effects of light levels on the spatiotemporal distribution of an open-space-foraging bat species show that even species considered to be “light tolerant”, that mainly roost in buildings (Marnell & Presetnik, 2010), can suffer from light pollution. Because bat species of the same foraging guild tend to respond to ALAN in a similar way (Voigt et al., 2021), other open-space-foraging bat species are likely to suffer from similar impacts of light pollution on their abundance and timing of activity. Narrow-space-foraging species that are known to be particularly sensitive toward ALAN (Rydell, 1992; Voigt et al., 2021) and/or species that usually roost in trees may experience even more drastic effects. It stresses the urge to reduce light pollution to protect bats, and more generally biodiversity.

Gaston et al., (2012) suggested five levers to reduce light pollution: prevent dark areas from being lit, limit the duration of artificial lighting, reduce light trespass, reduce light intensity and change ALAN spectral composition. Bats are known to present different responses to light with different spectra (Barré et al., 2021; Lewanzik & Voigt, 2017; Spoelstra et al., 2017; Straka et al., 2020). However, in this study, we could not assess how different spectral compositions would have affected our results, as the light pollution data available at landscape scale were not made of multiple spectral bands. Hence, further studies would particularly be necessary to

explore how ALAN spectral composition may modify how light pollution affects the timing of bat activity at landscape scale.

Limiting the lighting duration might only be efficient if part-night lighting schemes overlap with the range of bat activity (for instance streetlights should be switched off during emergence and during the first and higher foraging peak), which is not the case today (Azam et al., 2015; Day et al., 2015). As even low light intensities (similar to moonlight) could disrupt bat spatiotemporal distribution, the intensity under which light stops affecting bats might be very low. Therefore, even if reducing light intensity might reduce light impacts on bats, it might not be a very efficient measure. Our study, by highlighting that, at landscape scale, bats suffer from light pollution and its intensity variation due to cloud cover, shows the need of lighting installations that reduce horizontally- and upward-directed lighting, and more generally light trespass.

5. Conclusion

This study highlights that the abundance and timing of activity of an open-space-foraging bat species, at foraging sites, are both affected by light pollution at landscape scale. It stresses that even species often considered to be “light tolerant” could suffer from ALAN. The intensity under which light stops impacting bat activity could be very low as moonlight, cloud cover and the amplifying of skyglow during overcast nights seem to impact the spatiotemporal distribution of bats. By showing that the bat abundance was reduced and the timing of bat activity was delayed when exposed to light, our study raises the urge to investigate further how delayed timings of activity might affect individual fitness, reproduction success and eventually result in population dynamic disruptions.

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Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The data supporting this study are available at <https://doi.org/10.5281/zenodo.6418651>.

References

- Alaasam, V. J., Liu, X., Niu, Y., Habibian, J. S., Pieraut, S., Ferguson, B. S., Zhang, Y., & Ouyang, J. Q. (2021). Effects of dim artificial light at night on locomotor activity, cardiovascular physiology, and circadian clock genes in a diurnal songbird. *Environmental Pollution*, 282, 117036. <https://doi.org/10.1016/j.envpol.2021.117036>
- Amichai, E., & Kronfeld-Schor, N. (2019). Artificial Light at Night Promotes Activity Throughout the Night in Nesting Common Swifts (*Apus apus*). *Scientific Reports*, 9(1), 11052. <https://doi.org/10.1038/s41598-019-47544-3>
- Appel, G., López-Baucells, A., Magnusson, W. E., & Bobrowiec, P. E. D. (2017). Aerial insectivorous bat activity in relation to moonlight intensity. *Mammalian Biology*, 85, 37–46. <https://doi.org/10.1016/j.mambio.2016.11.005>
- Arthur, L., & Lemaire, M. (2015). *Les chauves-souris de France, Belgique, Luxembourg et Suisse*. Biotope ; Museum national d'Histoire Naturelle.
- 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? *Global Change Biology*, 21(12), 4333–4341. <https://doi.org/10.1111/gcb.13036>
- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., & Kerbiriou, C. (2018). Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning*, 175, 123–135. <https://doi.org/10.1016/j.landurbplan.2018.02.011>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., & Kerbiriou, C. (2016). Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity

- with a national-scale monitoring program. *Landscape Ecology*, 31(10), 2471–2483.
<https://doi.org/10.1007/s10980-016-0417-3>
- Barré, K., Kerbiriou, C., Ing, R.-K., Bas, Y., Azam, C., Le Viol, I., & Spoelstra, K. (2021). Bats seek refuge in cluttered environment when exposed to white and red lights at night. *Movement Ecology*, 9(1), 3. <https://doi.org/10.1186/s40462-020-00238-2>
- Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S. E., Julien, J.-F., Claireau, F., Kerbiriou, C., & Bas, Y. (2019). Accounting for automated identification errors in acoustic surveys. *Methods in Ecology and Evolution*, 10(8), 1171–1188.
<https://doi.org/10.1111/2041-210X.13198>
- Bas, Y., Bas, D., & Julien, J.-F. (2017). Tadarida: A Toolbox for Animal Detection on Acoustic Recordings. *Journal of Open Research Software*, 5(1), 6.
<https://doi.org/10.5334/jors.154>
- Bas, Y., Roemer, C., & Julien, J.-F. (2020). *Bat population trends*. Team-Chiro.
<https://croemer3.wixsite.com/teamchiro/population-trends?lang=fr>
- Boldogh, S., Dobrosi, D., & Samu, P. (2007). The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica*, 9(2), 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)
- Bowden, J., & Church, B. M. (1973). The influence of moonlight on catches of insects in light-traps in Africa. Part II. The effect of moon phase on light-trap catches. *Bulletin of Entomological Research*, 63(1), 129–142.
<https://doi.org/10.1017/S0007485300050938>
- Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2020). Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle: Light pollution and moth life cycles. *Insect Conservation and Diversity*, 14(2), 167–187. <https://doi.org/10.1111/icad.12447>
- Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2021). Street lighting has detrimental impacts on local insect populations. *Science Advances*, 7, eabi8322. <https://doi.org/10.1126/sciadv.abi8322>
- Bullock, D. J., Combes, B. A., Eales, L. A., & Pritchard, J. S. (1987). Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrellus*). *Journal of Zoology*, 211(2), 267–274. <https://doi.org/10.1111/j.1469-7998.1987.tb01533.x>
- Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and

- comparisons. *Behavioral Ecology and Sociobiology*, 65, 23–35.
<https://doi.org/10.1007/s00265-010-1029-6>
- Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96(9), 2370–2382. <https://doi.org/10.1890/14-1639.1>
- Catto, C. M. C., Hutson, A. M., Racey, P. A., & Stephenson, P. J. (1996). Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology*, 238(4), 623–633. <https://doi.org/10.1111/j.1469-7998.1996.tb05419.x>
- Catto, C. M. C., Racey, P. A., & Stephenson, P. J. (1995). Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, 235(4), 635–644. <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>
- Ciechanowski, M., Zając, T., Biłas, A., & Dunajski, R. (2007). Spatiotemporal variation in activity of bat species differing in hunting tactics: Effects of weather, moonlight, food abundance, and structural clutter. *Canadian Journal of Zoology*, 85(12), 1249–1263. <https://doi.org/10.1139/Z07-090>
- Cryan, P. M., Bogan, M. A., & Altenbach, J. S. (2000). Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy*, 81(3), 719–725. [https://doi.org/10.1644/1545-1542\(2000\)081<0719:EOEODO>2.3.CO;2](https://doi.org/10.1644/1545-1542(2000)081<0719:EOEODO>2.3.CO;2)
- Day, J., Baker, J., Schofield, H., Mathews, F., & Gaston, K. J. (2015). Part-night lighting: Implications for bat conservation: Part-night lighting and bats. *Animal Conservation*, 18(6), 512–516. <https://doi.org/10.1111/acv.12200>
- Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4, 164. <https://doi.org/10.3389/fphys.2013.00164>
- Dominoni, D. M., Quetting, M., & Partecke, J. (2013). Long-Term Effects of Chronic Light Pollution on Seasonal Functions of European Blackbirds (*Turdus merula*). *PLoS ONE*, 8(12), e85069. <https://doi.org/10.1371/journal.pone.0085069>
- Duvergé, P. L., Jones, G., Rydell, J., & Ransome, R. D. (2000). Functional significance of emergence timing in bats. *Ecography*, 23(1), 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- Elvidge, C. D., Baugh, K., Zhizhin, M., Hsu, F.-C., & Ghosh, T. (2017). VIIRS night-time lights. *International Journal of Remote Sensing*, 38(21), 5860–5879. <https://doi.org/10.1080/01431161.2017.1342050>

- Erkert, H. G. (1982). Ecological Aspects of Bat Activity Rhythms. In T. H. Kunz (Ed.), *Ecology of Bats* (pp. 201–242). Springer US. https://doi.org/10.1007/978-1-4613-3421-7_5
- Evans, J. A., Elliott, J. A., & Gorman, M. R. (2007). Circadian Effects of Light No Brighter Than Moonlight. *Journal of Biological Rhythms*, 22(4), 356–367. <https://doi.org/10.1177/0748730407301988>
- 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. *Science Advances*, 2(6), e1600377. <https://doi.org/10.1126/sciadv.1600377>
- Galipaud, M., Gillingham, M. A. F., David, M., & Dechaume-Moncharmont, F.-X. (2014). Ecologists overestimate the importance of predictor variables in model averaging: A plea for cautious interpretations. *Methods in Ecology and Evolution*, 5(10), 983–991. <https://doi.org/10.1111/2041-210X.12251>
- Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biological Reviews*, 88(4), 912–927. <https://doi.org/10.1111/brv.12036>
- Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). REVIEW: Reducing the ecological consequences of night-time light pollution: options and developments. *Journal of Applied Ecology*, 49(6), 1256–1266. <https://doi.org/10.1111/j.1365-2664.2012.02212.x>
- Gaston, K. J., Visser, M. E., & Hölker, F. (2015). The biological impacts of artificial light at night: The research challenge. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140133. <https://doi.org/10.1098/rstb.2014.0133>
- Gomes, D. G. E., Appel, G., & Barber, J. R. (2020). Time of night and moonlight structure vertical space use by insectivorous bats in a Neotropical rainforest: An acoustic monitoring study. *PeerJ*, 8, e10591. <https://doi.org/10.7717/peerj.10591>
- Griffin, D. R., & Lindsay, R. B. (1959). *Listening in the Dark*. *Physics Today*, 12(1), 42–42. <https://doi.org/10.1063/1.3060644>
- Grubisic, M., van Grunsven, R. H. A., Kyba, C. C. M., Manfrin, A., & Hölker, F. (2018). Insect declines and agroecosystems: Does light pollution matter?: Insect declines and agroecosystems. *Annals of Applied Biology*, 173(2), 180–189. <https://doi.org/10.1111/aab.12440>

- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions: Multimodel inference. *Journal of Evolutionary Biology*, 24(4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>
- Haddock, J. K., Threlfall, C. G., Law, B., & Hochuli, D. F. (2019). Light pollution at the urban forest edge negatively impacts insectivorous bats. *Biological Conservation*, 236, 17–28. <https://doi.org/10.1016/j.biocon.2019.05.016>
- Hale, J. D., Fairbrass, A. J., Matthews, T. J., Davies, G., & Sadler, J. P. (2015). The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats. *Global Change Biology*, 21(7), 2467–2478. <https://doi.org/10.1111/gcb.12884>
- Harbusch, C., & Racey, P. A. (2006). The sessile serotine: The influence of roost temperature on philopatry and reproductive phenology of *Eptesicus serotinus* (Schreber, 1774) (Mammalia: Chiroptera). *Acta Chiropterologica*, 8(1), 213–229.
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C. C., Henckel, D., Hänel, A., Kappeler, P. M., Völker, S., Schwope, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C., & Tockner, K. (2010). The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy. *Ecology and Society*, 15(4), 13. <https://doi.org/10.5751/ES-03685-150413>
- Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: A question of evolving, acclimatizing or coping with urban environmental stress. *Functional Ecology*, 29(7), 913–923. <https://doi.org/10.1111/1365-2435.12477>
- Jechow, A., Hölker, F., Kolláth, Z., Gessner, M. O., & Kyba, C. C. M. (2016). Evaluating the summer night sky brightness at a research field site on Lake Stechlin in northeastern Germany. *Journal of Quantitative Spectroscopy and Radiative Transfer*, 181, 24–32. <https://doi.org/10.1016/j.jqsrt.2016.02.005>
- Jechow, A., Kolláth, Z., Ribas, S. J., Spoelstra, H., Hölker, F., & Kyba, C. C. M. (2017). Imaging and mapping the impact of clouds on skyglow with all-sky photometry. *Scientific Reports*, 7(1), 6741. <https://doi.org/10.1038/s41598-017-06998-z>
- Jechow, A., Kyba, C. C. M., & Hölker, F. (2020). Mapping the brightness and color of urban to rural skyglow with all-sky photometry. *Journal of Quantitative Spectroscopy and Radiative Transfer*, 250, 106988. <https://doi.org/10.1016/j.jqsrt.2020.106988>
- 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(1318), 445–455.
<https://doi.org/10.1098/rstb.1994.0161>
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, E., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., ... Joseph, D. (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, 77(3), 437–472.
- Kempnaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial Night Lighting Affects Dawn Song, Extra-Pair Siring Success, and Lay Date in Songbirds. *Current Biology*, 20(19), 1735–1739. <https://doi.org/10.1016/j.cub.2010.08.028>
- Kerbiriou, C., Barré, K., Mariton, L., Pauwels, J., Zissis, G., Robert, A., & Le Viol, I. (2020). Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of Bats. *Diversity*, 12(4), 165. <https://doi.org/10.3390/d12040165>
- Kerbiriou, C., Bas, Y., Le Viol, I., Lorrillière, R., Mougnot, J., & Julien, J.-F. (2019a). Potential of bat pass duration measures for studies of bat activity. *Bioacoustics*, 28(2), 177–192. <https://doi.org/10.1080/09524622.2017.1423517>
- Kerbiriou, C., Bas, Y., Le Viol, I., Lorrillière, R., Mougnot, J., & Julien, J.-F. (2019b). Bat Pass Duration Measurement: An Indirect Measure of Distance of Detection. *Diversity*, 11(3), 47. <https://doi.org/10.3390/d11030047>
- Kervyn, T. (2001). *Ecology and ethology of the serotine bat, Eptesicus serotinus (Chiroptera, Vespertilionidae): Perspectives for the conservation of bats*. University of Liège.
- Koen, E. L., Minnaar, C., Roever, C. L., & Boyles, J. G. (2018). Emerging threat of the 21st century lightscape to global biodiversity. *Global Change Biology*, 24(6), 2315–2324. <https://doi.org/10.1111/gcb.14146>
- Kolkert, H., Smith, R., Rader, R., & Reid, N. (2020). Insectivorous bats foraging in cotton crop interiors is driven by moon illumination and insect abundance, but diversity benefits from woody vegetation cover. *Agriculture, Ecosystems & Environment*, 302, 107068. <https://doi.org/10.1016/j.agee.2020.107068>
- Kupprat, F., Hölker, F., & Kloas, W. (2020). Can skyglow reduce nocturnal melatonin concentrations in Eurasian perch? *Environmental Pollution*, 262, 114324. <https://doi.org/10.1016/j.envpol.2020.114324>
- 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. *Science Advances*, 3(11), e1701528. <https://doi.org/10.1126/sciadv.1701528>
- Kyba, C. C. M., Tong, K. P., Bennie, J., Birriel, I., Birriel, J. J., Cool, A., Danielsen, A., Davies, T. W., Outer, P. N. den, Edwards, W., Ehlert, R., Falchi, F., Fischer, J., Giacomelli, A., Giubbilini, F., Haaima, M., Hesse, C., Heygster, G., Hölker, F., ... Gaston, K. J. (2015). Worldwide variations in artificial skyglow. *Scientific Reports*, 5, 8409. <https://doi.org/10.1038/srep08409>
- Lacoeuilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., & Kerbiriou, C. (2014). The Influence of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. *PLoS ONE*, 9(10), e103042. <https://doi.org/10.1371/journal.pone.0103042>
- Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbiriou, C., Fonderflick, J., & Besnard, A. (2019). Reducing light pollution improves connectivity for bats in urban landscapes. *Landscape Ecology*, 34, 793–809. <https://doi.org/10.1007/s10980-019-00803-0>
- Lang, A. B., Kalko, E. K. V., Römer, H., Bockholdt, C., & Dechmann, D. K. N. (2006). Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia*, 146, 659–666. <https://doi.org/10.1007/s00442-005-0131-3>
- Le Tallec, T., Théry, M., & Perret, M. (2015). Effects of light pollution on seasonal estrus and daily rhythms in a nocturnal primate. *Journal of Mammalogy*, 96(2), 438–445. <https://doi.org/10.1093/jmammal/gyv047>
- Lewanzik, D., & Voigt, C. C. (2017). Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *Journal of Applied Ecology*, 54(1), 264–271. <https://doi.org/10.1111/1365-2664.12758>
- Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, 2(4), 191–198. [https://doi.org/10.1890/1540-9295\(2004\)002\[0191:ELP\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2)
- Luo, B., Xu, R., Li, Y., Zhou, W., Wang, W., Gao, H., Wang, Z., Deng, Y., Liu, Y., & Feng, J. (2021). Artificial light reduces foraging opportunities in wild least horseshoe bats. *Environmental Pollution*, 288, 117765. <https://doi.org/10.1016/j.envpol.2021.117765>
- Lynn, K. D., Quintanilla-Ahumada, D., Anguita, C., Widdicombe, S., Pulgar, J. M., Manríquez, P. H., Quijón, P. A., & Duarte, C. (2021). Artificial light at night alters the activity and feeding behaviour of sandy beach amphipods and pose a threat to their ecological role in Atlantic Canada. *Science of The Total Environment*, 780, 146568. <https://doi.org/10.1016/j.scitotenv.2021.146568>

- Marnell, F., & Presetnik, P. (2010). *Protection of overground roosts for bats*.
UNEP/EUROBATS.
- Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., & Langton, S. (2015).
Barriers and benefits: Implications of artificial night-lighting for the distribution of
common bats in Britain and Ireland. *Philosophical Transactions of the Royal Society
B: Biological Sciences*, 370(1667), 20140124. <https://doi.org/10.1098/rstb.2014.0124>
- McAney, C. M., & Fairley, J. S. (1988). Activity patterns of the lesser horseshoe bat
Rhinolophus hipposideros at summer roosts. *Journal of Zoology*, 216(2), 325–338.
<https://doi.org/10.1111/j.1469-7998.1988.tb02433.x>
- McCain, C. M. (2007). Could temperature and water availability drive elevational species
richness patterns? A global case study for bats. *Global Ecology and Biogeography*,
16(1), 1–13. <https://doi.org/10.1111/j.1466-822X.2006.00263.x>
- McKinney, M. L. (2002). Urbanization, Biodiversity, and Conservation. *BioScience*, 52(10),
883–890. [https://doi.org/10.1641/0006-3568\(2002\)052\[0883:UBAC\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)
- Millon, L., Julien, J.-F., Julliard, R., & Kerbiriou, C. (2015). Bat activity in intensively
farmed landscapes with wind turbines and offset measures. *Ecological Engineering*,
75, 250–257. <https://doi.org/10.1016/j.ecoleng.2014.11.050>
- Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K., & Seymoure, B. M.
(2019). Light pollution is a driver of insect declines. *Biological Conservation*, 241,
108259. <https://doi.org/10.1016/j.biocon.2019.108259>
- Pauwels, J., Le Viol, I., Azam, C., Valet, N., Julien, J.-F., Bas, Y., Lemarchand, C., Sánchez
de Miguel, A., & Kerbiriou, C. (2019). Accounting for artificial light impact on bat
activity for a biodiversity-friendly urban planning. *Landscape and Urban Planning*,
183, 12–25. <https://doi.org/10.1016/j.landurbplan.2018.08.030>
- Pauwels, J., Le Viol, I., Bas, Y., Valet, N., & Kerbiriou, C. (2021). Adapting street lighting to
limit light pollution's impacts on bats. *Global Ecology and Conservation*, 28, e01648.
<https://doi.org/10.1016/j.gecco.2021.e01648>
- Put, J. E., Fahrig, L., & Mitchell, G. W. (2019). Bats respond negatively to increases in the
amount and homogenization of agricultural land cover. *Landscape Ecology*, 34(8),
1889–1903. <https://doi.org/10.1007/s10980-019-00855-2>
- R Core Team. (2015). *R: A language and environment for statistical computing* (3.2.3)
[Computer software]. R Foundation for Statistical Computing. URL [https://www.R-
project.org/](https://www.R-project.org/)

- R Core Team. (2021). *R: A language and environment for statistical computing* (4.0.4.) [Computer software]. R Foundation for Statistical Computing. URL <https://www.R-project.org/>
- Raap, T., Pinxten, R., & Eens, M. (2015). Light pollution disrupts sleep in free-living animals. *Scientific Reports*, 5, 13557. <https://doi.org/10.1038/srep13557>
- Richards, S. A. (2007). Dealing with overdispersed count data in applied ecology: Overdispersed count data. *Journal of Applied Ecology*, 45(1), 218–227. <https://doi.org/10.1111/j.1365-2664.2007.01377.x>
- Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65(1), 77–89. <https://doi.org/10.1007/s00265-010-1035-8>
- Robinson, M. F., & Stebbings, R. E. (1997). Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *Journal of Zoology*, 243(1), 117–136. <https://doi.org/10.1111/j.1469-7998.1997.tb05759.x>
- Rotics, S., Dayan, T., & Kronfeld-Schor, N. (2011). Effect of artificial night lighting on temporally partitioned spiny mice. *Journal of Mammalogy*, 92(1), 159–168. <https://doi.org/10.1644/10-MAMM-A-112.1>
- 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. *Environmental Pollution*, 252(Part B), 1671–1677. <https://doi.org/10.1016/j.envpol.2019.06.105>
- Russo, D., & Jones, G. (2003). Use of foraging habitats by bats in a Mediterranean area determined by acoustic surveys: Conservation implications. *Ecography*, 26(2), 197–209. <https://doi.org/10.1034/j.1600-0587.2003.03422.x>
- Rydell, J. (1992). Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology*, 6(6), 744–750. <https://doi.org/10.2307/2389972>
- Rydell, J., Entwistle, A. C., & Racey, P. A. (1996). Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk. *Oikos*, 76(2), 243–252. <https://doi.org/10.2307/3546196>
- Saldaña-Vázquez, R. A., & Munguía-Rosas, M. A. (2013). Lunar phobia in bats and its ecological correlates: A meta-analysis. *Mammalian Biology*, 78(3), 216–219. <https://doi.org/10.1016/j.mambio.2012.08.004>
- Salinas-Ramos, V. B., Ancillotto, L., Cistrone, L., Natasi, C., Bosso, L., Smeraldo, S., Sánchez-Cordero, V., & Russo, D. (2021). Artificial illumination influences niche

- segregation in bats. *Environmental Pollution*, 284, 117187.
<https://doi.org/10.1016/j.envpol.2021.117187>
- Salvarina, I., Gravier, D., & Rothhaupt, K.-O. (2018). Seasonal bat activity related to insect emergence at three temperate lakes. *Ecology and Evolution*, 8(7), 3738–3750.
<https://doi.org/10.1002/ece3.3943>
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041-210X.2010.00012.x>
- Secondi, J., Mondy, N., Gippet, J. M. W., Touzot, M., Gardette, V., Guillard, L., & Lengagne, T. (2021). Artificial light at night alters activity, body mass, and corticosterone level in a tropical anuran. *Behavioral Ecology*, arab044.
<https://doi.org/10.1093/beheco/arab044>
- Seto, K. C., Guneralp, B., & Hutyrá, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109(40), 16083–16088.
<https://doi.org/10.1073/pnas.1211658109>
- 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. *Proceedings of the Royal Society B: Biological Sciences*, 284(1855), 20170075. <https://doi.org/10.1098/rspb.2017.0075>
- Stone, E. L., Harris, S., & Jones, G. (2015). Impacts of artificial lighting on bats: A review of challenges and solutions. *Mammalian Biology*, 80(3), 213–219.
<https://doi.org/10.1016/j.mambio.2015.02.004>
- Stone, E. L., Jones, G., & Harris, S. (2009). Street Lighting Disturbs Commuting Bats. *Current Biology*, 19(13), 1123–1127. <https://doi.org/10.1016/j.cub.2009.05.058>
- Straka, T. M., Greif, S., Schultz, S., Goerlitz, H. R., & Voigt, C. C. (2020). The effect of cave illumination on bats. *Global Ecology and Conservation*, 21, e00808.
<https://doi.org/10.1016/j.gecco.2019.e00808>
- Svechkina, A., Portnov, B. A., & Trop, T. (2020). The impact of artificial light at night on human and ecosystem health: A systematic literature review. *Landscape Ecology*, 35, 1725–1742. <https://doi.org/10.1007/s10980-020-01053-1>
- Tiede, J., Diepenbruck, M., Gadau, J., Wemheuer, B., Daniel, R., & Scherber, C. (2020). Seasonal variation in the diet of the serotine bat (*Eptesicus serotinus*): A high-

- resolution analysis using DNA metabarcoding. *Basic and Applied Ecology*, S1439179120300992. <https://doi.org/10.1016/j.baae.2020.09.004>
- Torres, D., Tidau, S., Jenkins, S., & Davies, T. W. (2020). Artificial skyglow disrupts celestial migration at night. *Current Biology*, 30(12), R696–R697. <https://doi.org/10.1016/j.cub.2020.05.002>
- van Grunsven, R. H. A., van Deijk, J. R., Donners, M., Berendse, F., Visser, M. E., Veenendaal, E. M., & Spoelstra, K. (2020). Experimental light at night has a negative long-term impact on macro-moth populations. *Current Biology*, 30(12), R694–R695. <https://doi.org/10.1016/j.cub.2020.04.083>
- van Hasselt, S. J., Hut, R. A., Allocca, G., Vyssotski, A. L., Piersma, T., Rattenborg, N. C., & Meerlo, P. (2021). Cloud cover amplifies the sleep-suppressing effect of artificial light at night in geese. *Environmental Pollution*, 273, 116444. <https://doi.org/10.1016/j.envpol.2021.116444>
- Vásquez, D. A., Grez, A. A., & Rodríguez-San Pedro, A. (2020). Species-specific effects of moonlight on insectivorous bat activity in central Chile. *Journal of Mammalogy*, 101(5), gyaa095. <https://doi.org/10.1093/jmammal/gyaa095>
- Vaughan, N., Jones, G., & Harris, S. (1997). Habitat Use by Bats (Chiroptera) Assessed by Means of a Broad-Band Acoustic Method. *Journal of Applied Ecology*, 34(3), 716–730. <https://doi.org/10.2307/2404918>
- Verboom, B., & Huitema, H. (1997). The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology*, 12, 117–125. <https://doi.org/10.1007/BF02698211>
- Voigt, C. C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens, H. J. G. A., Mathews, F., Rydell, J., Spoelstra, K., & Zagamajster, M. (2021). The Impact Of Light Pollution On Bats Varies According To Foraging Guild And Habitat Context. *BioScience*, 71(10), 1103–1109. <https://doi.org/10.1093/biosci/biab087>
- Voigt, C. C., Scholl, J. M., Bauer, J., Teige, T., Yovel, Y., Kramer-Schadt, S., & Gras, P. (2020). Movement responses of common noctule bats to the illuminated urban landscape. *Landscape Ecology*, 35, 189–201. <https://doi.org/10.1007/s10980-019-00942-4>
- Williams, C. B., & Singh, B. P. (1951). Effect of Moonlight on Insect Activity. *Nature*, 167(4256), 853. <https://doi.org/10.1038/167853a0>

- Wilson, A. A., Seymoure, B. M., Jaeger, S., Milstead, B., Payne, H., Peria, L., Vosbigian, R., & Francis, C. D. (2021). Direct and ambient light pollution alters recruitment for a diurnal plant-pollinator system. *Integrative and Comparative Biology*, 31(3), 1122–1133. <https://doi.org/10.1093/icb/icab010>
- 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. *Global Change Biology*, 24(12), 5909–5918. <https://doi.org/10.1111/gcb.14462>
- Zissis, G., Bertoldi, P., & Serrenho, T. (2021). *Update on the status of LED-lighting world market since 2018* (JRC Technical Report EUR 30500 EN). Publications Office of the European Union. <https://data.europa.eu/doi/10.2760/759859>
- Zuckerberg, B., Cohen, J. M., Nunes, L. A., Bernath-Plaisted, J., Clare, J. D. J., Gilbert, N. A., Kozidis, S. S., Maresh Nelson, S. B., Shipley, A. A., Thompson, K. L., & Desrochers, A. (2020). A Review of Overlapping Landscapes: Pseudoreplication or a Red Herring in Landscape Ecology? *Current Landscape Ecology Reports*, 5(4), 140–148. <https://doi.org/10.1007/s40823-020-00059-4>

Supplementary material (*available in the Appendix II at the end of this PhD*)

Supplementary material A: Consistency of the results obtained for datasets built with a maximum error rate tolerance of 0.5 with datasets built with a maximum error rate tolerance of 0.1

Supplementary material B: Threshold on the number of *E. serotinus* passes for the “timing of activity” analyses

Supplementary material C: Comparison of the French radiance gradient with the radiance gradient in our datasets

Supplementary material D: Influence of the spatial scale at which the ALAN metric is calculated

Supplementary material E: Details the calculation and selection of environmental variables

Supplementary material F: Gradient of cloud cover for the studied nights

Supplementary material G: Gradient of moonlight for the studied nights

Table H: Variables extracted to control exogenous factors that could impact *E. serotinus* relative abundance and timing of activity at their foraging site. The variables that have been discarded due to multi-collinearity issues are in brackets. Ab = “relative abundance” dataset, Ta = “timing of activity” dataset.

Supplementary material I: Checks of model assumptions

Supplementary material J: Analyses when considering full models without interactions including ALAN

Supplementary material K: Checking of the robustness of the model averaging results

Table L: Results of the model averaging for the “relative abundance” and the “timing of activity” analyses. Even if a lot of models were selected in these analyses, the differences between the AICc of the null model and the AICc of the best model were always high.

Table M: Mean of the mean radiances (in $\text{nW} \cdot \text{sr}^{-1} \cdot \text{cm}^{-2}$) of the French municipalities according to their population size (only municipalities that are below 500 m above sea levels are considered).

Figure N: Interaction between cloud cover and ALAN: Predicted values and 95% confidence intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they were previously scaled) apart from cloud cover and ALAN. This graph represents the median time of activity according to cloud cover (back transformed in %) for three values of ALAN ($2.2 \text{ nW} \cdot \text{sr}^{-1} \cdot \text{cm}^{-2}$ being the mean radiance of French municipalities of 1000 to 5000 inhabitants and $7.8 \text{ nW} \cdot \text{sr}^{-1} \cdot \text{cm}^{-2}$ being the mean radiance for municipalities of 5000 to 10,000 inhabitants, see Table M).

Figure O: Interaction between ALAN and moonlight: Predicted values and 95% confidence intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they were previously scaled) apart from ALAN and moonlight. This graph represents the median time of activity according to ALAN (radiance back transformed in $\text{nW} \cdot \text{sr}^{-1} \cdot \text{cm}^{-2}$) for three values of moonlight.

In short

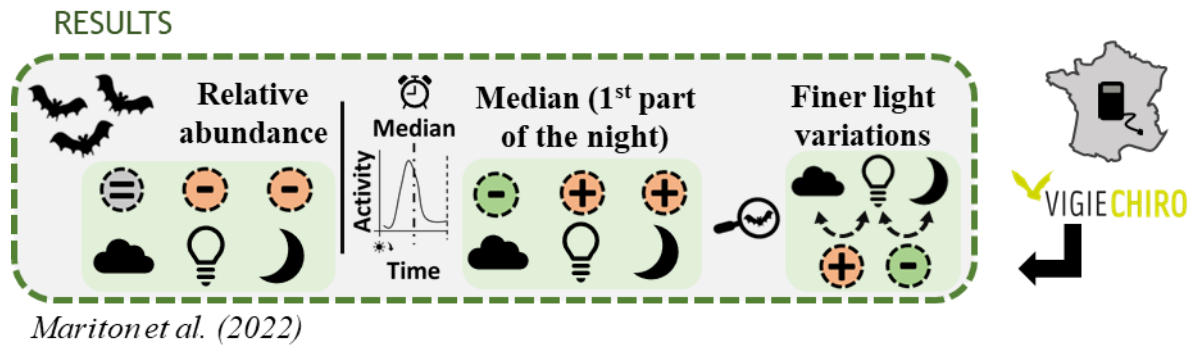


Figure 22: Results of Mariton et. al (2022)

Main novelties:

- Delay effect due to both natural and artificial light on:
 - (1) the timing of activity of an open-space-foraging bat species,
 - (2) the timing of activity of a bat species at the landscape scale.
- Low intensities matter:
 - (1) moonlight negatively affected the abundance of an open-space-foraging bat species,
 - (2) moonlight, cloud cover and the amplification of skyglow during overcast nights negatively impacted the timing of activity of a bat species.

Results (Figure 22):

During gestation, ALAN, and to a lesser extent moonlight, reduced *E. serotinus* abundance at the landscape scale. ALAN delayed activity, and this delay was amplified during overcast nights. On the contrary, where there was no ALAN, the higher the cloud cover, the earlier the activity occurred. Cloud cover likely darkened the night sky in rural locations, whereas it amplified the skyglow in light-polluted places, thus increasing ALAN effects on bats. Moonlight also delayed activity but this effect was weakened in light-polluted landscapes. Our study shows that even fine variations of light levels can affect the spatiotemporal distribution of a common species usually considered to be “light tolerant”, with potential cascading effects on individual fitness and population dynamics.

Perspectives

In this second chapter, we showed that light levels, even at low intensities, negatively affect the abundance of an open-space-foraging bat species and delay its timing of activity. Although this study highlights a potential new mechanism by which light pollution could be detrimental to bats (even those which are considered to be “light tolerant”), it raises many new questions.

Firstly, the reason for this delaying effect remains to be explained. One explanation may be that, because of the reduced landscape connectivity in light-polluted areas, bats have to travel longer to reach their foraging sites. According to previous studies on narrow-space-foraging species (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021), a later arrival at foraging sites could also be a direct consequence of a later emergence from roosts. During this PhD, a field session was conducted to test this hypothesis on *E. serotinus* and on *R. ferrumequinum*, the field issues and prospects it raised are presented in **Box 5** (e.g. *How to measure light pollution in the field? How to monitor bat emergence from roosts with passive acoustic devices?*).

It has been suggested that bats may emerge later from their roosts when exposed to light because of an increased perception of predation risk, regardless to the real presence of a predator (Boldogh et al., 2007; Duvergé et al., 2000; Luo et al., 2021). Another explanation could be that, by masking natural light-dark cycles, ALAN alters the circadian clock of bats. However, so far, this potential effect of light pollution the clock of bats has never been studied.

Secondly, the consequences of a delay in *E. serotinus* activity need to be investigated. In particular, further studies should focus on whether this shift can be compensated for by bats – by being active later in the night for instance, at times when they are not usually active – or whether it cannot be compensated for. From what we know so far about on *E. serotinus*, the latter seems the more likely hypothesis.

Indeed, as Jones and Rydell (1994) hypothesised, bat diel activity pattern is probably constrained by a trade-off between (1) avoiding predation and thus avoiding being active too early when predators can take advantage of light to locate bats, (2) exploiting the activity peak of the insects on which bats feed. Previous studies have shown that *E. serotinus* is a species feeding predominantly on Coleoptera (Jones and Rydell, 1994; Robinson and Stebbings, 1993; Ware et al., 2020, however see also Tiede et al., 2020 who found a less specialised diet). As shown in the first chapter of this PhD, the diel activity pattern of *E. serotinus* has the particularity to be concentrated in a single peak of activity at the beginning of the night (more

than half of its activity occurs in the first third of the night) (**Figure 23**). Such a diel activity pattern is consistent with a specialised diet that would require this species to be active early in the night despite predation risks and to concentrate its main foraging bout during a relatively short period.

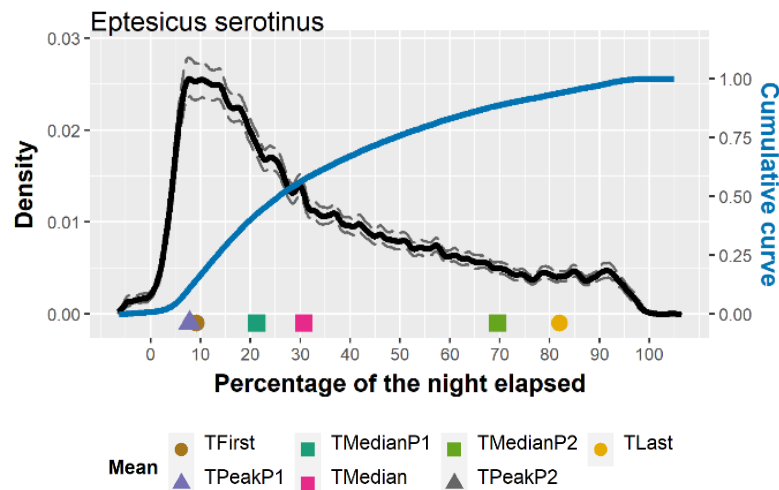


Figure 23 : Activity distribution throughout the night for *E. serotinus*. In black, estimated density of activity according to the percentage of the night elapsed. In blue, cumulative curve of weighted bat activity. The dashed lines represent the 95 % confidence bands for the estimated density. The symbols represent the mean times of the key descriptors and the times of the activity peaks detected.

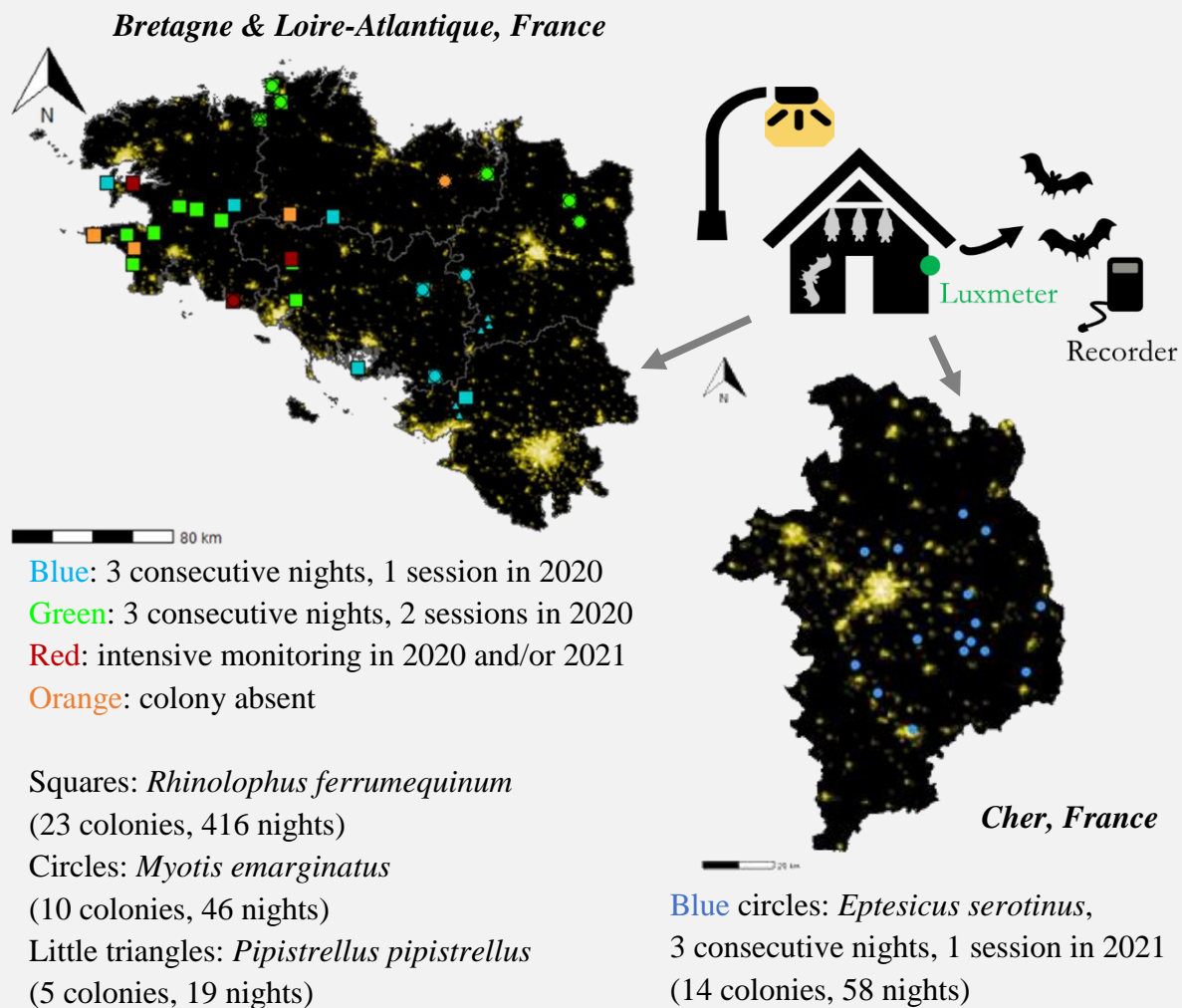
Source: Mariton et al. (*accepted*)

Therefore, a shift of *E. serotinus* activity later at night could desynchronise their peak of activity with the peak of activity of their prey and reduce their efficient time-budget (i.e. reduce the period during which *E. serotinus* can feed on the prey that mainly composed their diets). In the long term, it could then have a negative impact on individual fitness and population dynamics, and thus explain, at least partially, the lower abundance of *E. serotinus* at the landscape scale we found. This link remains to be proven and should be the focus of future studies.

Eventually, it should be noted that we focused on the gestation period of *E. serotinus*. As a matter of fact, Catto et al., (1995) showed that while the timing of *E. serotinus* activity was unimodal to bimodal during gestation, it became more complex and multimodal during lactation. As we wanted to focus on a period during which the timing of *E. serotinus* activity would be consistent, we only studied gestation. However, in the first chapter of this PhD, we showed that despite variations in the peak amplitude, *E. serotinus* activity remains unimodal throughout the year. Thus, the study of the impact of light pollution on *E. serotinus* timing of activity during lactation would be of great interest.



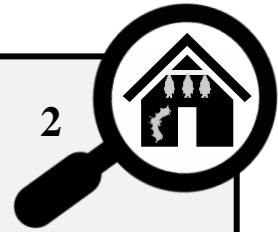
Box 5: A field session initiating wider questions on bat monitoring methods and light data acquisition



Data acquisition in (a) Bretagne and Loire-Atlantique, (b) the Cher, with the collaboration of: the Groupe Mammalogique Breton, Bretagne Vivante, Amikiro, the Muséum d'histoire naturelle de Bourges.

How to design a sampling of roosts along a light pollution gradient?

The species the most commonly monitored by local associations are often those that roost in made-made structures and that present high conservation stakes. They are then often narrow-space-foraging species, such as *Rhinolophus* spp. and most *Myotis* spp., which are “light intolerant” and may not even roost in light-polluted areas, even if light levels are low. For example, we found almost not roost of *R. hipposideros* in light-polluted areas, which led to the abandonment of the project to focus on this species. *E. serotinus* has even been observed to leave its roosts when exposed to ALAN (Arthur and Lemaire, 2015). These observations suggest that the valuable bat roost locations collected by local associations can be used in the future to assess



2

Box 5: A field session initiating wider questions on bat monitoring methods and light data acquisition

ALAN effect on roost selection and to determine the light pollution gradient tolerated by bat species around their roosts. Indeed, to date, most studies dealing with roost selection have focused on roost intrinsic characteristics, whereas few studies have investigated the spatial distribution of roosts in order to identify how habitat selection could drive bats' choice of roost (Arthur et al., 2014). Without this knowledge, we could only hypothesise that the roosts we selected were representative of the light pollution gradient tolerated by the studied species.

How to measure light levels around roosts?

As identified by Hölker et al. (2021) the choice of a light measurement method when studying the effect of light pollution on biodiversity remains a major issue. In practice, the cost and complexity of sophisticated light measurement devices lead ALAN researchers to opt for more conventional devices in ecological studies, in particular lux meters (Hölker et al., 2021). They measure illuminance in lux and are thus based on the sensitivity of the human eye and not on the organisms studied (see **Box 1**). They also have the disadvantage of low sensitivity and accuracy at low light levels (Hänel et al., 2018). Nevertheless, as lighting engineers mainly used them, this facilitates the transfer of research to policy (Hölker et al., 2021). They are also among the most affordable light measurement devices (Hänel et al., 2018). We then measured local light levels using lux meters but, to overcome the often-limited temporal range of light measurement in ecological studies (Hölker et al., 2021), we used dataloggers that took a measure every 30 seconds during the monitored nights. As they were directional, we fixed them in such a way that they reflected what a bat might see when emerging from its roost.

To get a better overview of the levels of diffuse light pollution around three colonies that we monitored intensively, we also measured the night sky brightness at the zenith every minute using sky quality meters called “Ninox”. These devices were used in Deverchère et al. (2022) to design a statistical indicator of light pollution that they called *NSB Dispersion Ratio*.

Eventually, this field session brought us to face with the pressing need to **standardise light measurement methods** highlighted by Hölker et al. (2021). In particular, we felt the need for **interdisciplinary collaborations** as ecologists often lack the knowledge to understand radiometry and photometry and thus select appropriate measurement approaches and devices for their studies.



Box 5: A field session initiating wider questions on bat monitoring methods and light data acquisition

How to monitor when bat leave or enter their roost?

The previous studies on bat diel activity patterns at roost mainly used visual counts, radiotracking devices or infra-red cameras (see *Appendix A* of Mariton et al. (*accepted*), in the *Appendix I* of this PhD thesis). Although providing very accurate data, these methods are often limited by the price of the devices, the high effort of on-site survey required and/or the time needed to process the data after acquisition. Conversely, **passive acoustic monitoring** (PAM) requires minimum on-site survey effort while the time required to process the collected data is reduced thanks to the development of automated identification software (Revilla-Martín et al., 2020). During this field session, we used passive acoustic recorders that were placed: (1) not too close to the colony so as not to record activity inside the roost, (2) not too far from the exit so that bat exits and entrances were recorded. However, other limitations and possible biases remained. For instance, especially for common species such as *P. pipistrellus*, the recorder probably detected bats that were nearby but not from the targeted colony. For species like *R. ferrumequinum*, circling and light-testing behaviours prior to emergence could be recorded although there were not true exits. As proposed by Revilla-Martín et al. (2020), to overcome this issue and determine whether bats are exiting or entering their roosts, the use of **two microphones in stereo** (Claireau et al., 2019) could be an interesting prospect that has not been explored yet.

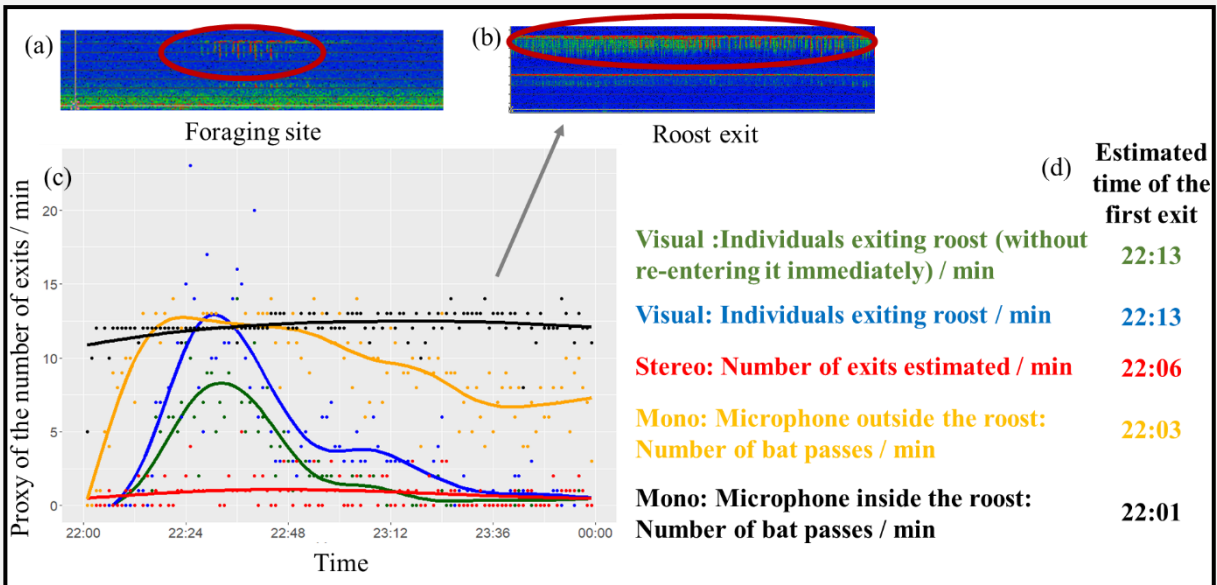
How to determine the timing of activity at roosts? (case study of the first emergence)

Very few studies have used yet PAM to determine bat activity pattern at roosts, so defining a method and a metric that would be a **robust proxy for the actual timing of activity** was a methodological issue. At one roost, during three evenings, we thus simultaneously carried out visual counts, passive acoustic monitoring using one microphone (“mono” approach) and using two microphones (“stereo” approach). Bat activity was then estimated using “bat passes” (i.e. a single or several calls of the same bat species during 5-sec interval).

The “mono” approach was limited by the saturation of the number of bat passes per minutes (according to the time division of the sound files, saturation occurred when about $60 / 5 = 12$ bat passes per min were found). The stereo recordings were processed according to the methodology of Claireau et al. (2019) which allows the detection of bat crossings based on an acoustic flight path reconstruction approach. However, it was only designed for situations



Box 5: A field session initiating wider questions on bat monitoring methods and light data acquisition



*Monitoring the emergence of *R. ferrumequinum* at roost during one night: a bat pass recorded (a) at a foraging site, (b) at the roost exit, (c) estimation of the number of exits per minute according to the different methods (the visual count not considering bats that immediately re-entered the roost is considered as the reference), (d) estimated time of the first exit.*

when a bat call recorded in a microphone can be associated with the same call in the other. During emergence, as the bats' calls were emitted continuously, it was almost impossible, hence the very low number of exits detected in stereo. However, with regard to the characterisation of the timing of activity the **“stereo” approach provided better results** than the “mono” approach, with a better estimate of the time of the first pass.

These results show that traditional metrics of activity (e.g. bat passes) may not be suitable for studies at roosts and raise the need to test other metrics. For example, the Tadarida software provide, for each bat pass, the time at which the call starts inside the 5-sec file and at which it ends. It is then possible to calculate a duration of bat calls per minutes during emergence. By doing so, we thus assessed when bat calls start to be continuous for the 101 nights during which we monitored a *R. ferrumequinum* roost. For these nights, activity started to be continuous from 7 min before sunset, to 22 min after sunset (standard deviation = 6.7 min). This metric provided the best estimate of the time of the first exit in the example presented above (22:09). Thus, **the design of metrics adapted to the particularities of bat activity at roosts** is an encouraging prospect that should be the focus of further explorations.

Indeed, bats may show different responses to light pollution depending on the time of the year. During pregnancy, female bats experience a greater wing loading which may affect their flight performance and make them more likely to be vulnerable to predation (Duvergé et al., 2000). The potential trade-off between energy requirements and predation risks could then lead to delayed emergence because of light pollution. During lactation, reproductive female bats have many constraints: their energy requirements are the highest of the year (Racey and Speakman, 1987), they must divide their time between foraging and suckling their young and they must cope with short night length. They may then not be able to adapt their timing of activity to the presence of light pollution and be active despite predation risks.

Another limitation of this study is that it focuses on only one species. However, we hypothesised that other open-space-foraging bat species are likely to suffer from similar impacts of light pollution on their abundance and timing of activity. Indeed, it has been shown that bat species of the same foraging guild tend to respond to ALAN in a similar way (Voigt et al., 2021). To test this hypothesis, we conducted preliminary analyses, similar to those of the paper we presented in this chapter, on eight open- and edge-space-foraging species during both gestation and lactation (see results **Box 6**). For four of the species studied, our preliminary results indicated that ALAN could negatively affect their abundance and/or delayed their timing of activity during gestation and/or lactation.

With regard to conservation, our results show that even a species usually considered to be light tolerant is negatively affected by ALAN. It has been shown that *E. serotinus* populations have declined by 30 % between 2004 and 2019, without any geographic variation on the national territory (Bas et al., 2020). This decline is therefore very worrying and protecting this bat species from anthropogenic pressures seems to be an urgent matter. Reducing the duration of lighting so as not to switch on lights during the main activity peak of *E. serotinus* would mean starting PNL schemes very early, which would probably not be accepted by local people. Thus, other light pollution mitigation measures should be implemented where and when lights cannot be switched off.

In our study, *E. serotinus* was even affected by moonlight, suggesting that the intensity threshold below which ALAN ceases having an impact on this species may be very low. However, *E. serotinus* responded to fine variations of light levels as the amplification of the skyglow during overcast nights. Thus, reducing light intensity might attenuate (but not eliminate) local impacts of ALAN, while, at the landscape scale, reducing light intensity and trespass could be beneficial by helping to reduce the intensity and the extent of the skyglow. The last lever, would be to work on the emission spectrum of light sources and to choose the

one that would be the least harmful for bats. In particular, nowadays, obsolete lighting equipment is being progressively phased-out and replaced by broad spectrum LEDs in developed countries. However, to date, few studies have investigated the effect of switching from old lighting technologies to LEDs.

Box 6: Impact of light pollution on the abundance and timing of activity of open- and edge-space-foraging bat species at landscape scale (in prep)

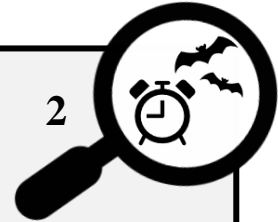


Context:

In this study, we intended to assess the **impact of light pollution on the spatiotemporal distribution** of eight bat species (*E. serotinus*, *N. noctula*, *N. leisleri*, *M. daubentonii*, *P. kuhlii*, *P. nathusii*, *P. pipistrellus* and *P. pygmaeus*), among the most common in France, at the landscape scale. These species are open- (*E. serotinus*, *N. noctula* and *N. leisleri*) and edge-space-foragers (*M. daubentonii*, *P. kuhlii*, *P. nathusii*, *P. pipistrellus*, *P. pygmaeus*), and are therefore part of two guilds of **species usually considered to be “light tolerant”** (Voigt et al., 2021). As a matter of fact, with the exception of *M. daubentonii*, locally these species are known to be able to feed on insect aggregation at light sources. However, at the landscape scale, their responses to ALAN appear to be more complex, and even dependent on the context or behaviour considered (Azam et al., 2016; Barré et al., 2021; Laforge et al., 2019; Mathews et al., 2015; Pauwels et al., 2019; Voigt et al., 2020).

While most of these species are considered common or even very common in France, it should be noted that *N. noctula* is classified as “vulnerable” in France, while *E. serotinus*, *N. leisleri*, *P. nathusii* and *P. pipistrellus* are classified as “near threatened” (UICN France et al., 2017). Thus, determining whether light pollution is likely to have a negative impact on their populations is a major issue. Studies conducted locally allow us to assess how ALAN can modify these species’ behaviours, whereas **considering the landscape scale** allows to infer the possible impacts of light pollution on population dynamics (Azam et al., 2016).

Thus, using the **Vigie-Chiro dataset**, we assessed the impact of light pollution on the **abundance** and the **timing of activity** of these species at the landscape scale during two key periods for population dynamics but with different energy requirements: **gestation and lactation**. Considering the spatial and the temporal dimensions seems essential as it may highlight response mechanisms that may differ according to the niches of the different species studied (e.g. some species may not be able to adapt their timing of activity to light pollution and thus systematically avoid lit sites, while others may favour a temporal shift in their activity



Box 6: Impact of light pollution on the abundance and timing of activity of open- and edge-space-foraging bat species at landscape scale (in prep)

in order to continue to exploit the same specific foraging habitats).

Materials and Methods:

We applied a **method similar to the one used in Mariton et al. (2022)**, with slight variations on the data curation and the statistical analyses. The main difficulty in this study, as in Mariton et al. (2022), was to disentangle the effect of ALAN from the effect of artificialized surfaces despite their high correlation, hence the choice to use model averaging.

See Appendix III for more details on the Materials and Methods

Preliminary results and discussion:

***Our results are only preliminary** as, despite our precautions, (1) some temporal and/or spatial autocollinearity remain for some species, (2) first checking of model assumptions showed that some assumptions could have been violated for some species, (3) we have not integrated yet interactions that can reflect small variations of light intensity. However, we believe that some findings are already of interest.*

We found that the **relative abundance** of *E. serotinus* was negatively impacted by **ALAN** during both gestation and lactation. Only the relative abundance of *M. daubentonii* also responded to ALAN, it decreased in light polluted landscapes. It could then appear that the five-remaining edge- and open-space-foraging species were not sensible to ALAN. However, apart from *P. pipistrellus*, all the other species responded positively to artificialized surfaces during gestation and/or lactation. Due to our modelling approach, for these species it cannot be ruled out that ALAN had an effect on them, but it was not detected because the overall positive effect of artificialized surfaces was stronger. Interestingly, the negative effect of **moonlight** on the relative abundance of *N. leisleri*, *P. nathusii* and *P. pygmaeus* can suggest that these species are more sensible to light than what our results suggested at first sight, at least when their energetic needs are not as high as during lactation.

Regarding **ALAN** effect on bat **timing of activity**, we found a delaying effect on *E. serotinus*, *N. noctula* and *P. pipistrellus* but only during gestation. The disappearance of this effect during lactation suggests that bat timing of activity is partly driven by a trade-off between energetic needs and predation risks. During gestation higher vulnerability to predation due to greater wing loading might lead bats to avoid predation risks, and hence delay



Box 6: Impact of light pollution on the abundance and timing of activity of open- and edge-space-foraging bat species at landscape scale (in prep)

Preliminary results: responses of the eight species studied to ALAN, Moonlight and Artificialized surfaces (effect in the table only if “significant”, i.e. if sum of weight > 0.6 and confidence interval that did not overall zero)

ALAN *	Relative abundance		TMedianP1	
	Gestation	Lactation	Gestation	Lactation
<i>E. serotinus</i>	-0.45	-0.42	665.94	/
<i>M. daubentonii</i>	/	-0.64	/	/
<i>N. leisleri</i>	/	/	/	/
<i>N. noctula</i>	/	/	1083.31	/
<i>P. kuhlii</i>	/	/	/	/
<i>P. nathusii</i>	/	/	/	/
<i>P. pipistrellus</i>	/	/	435.57	/
<i>P. pygmaeus</i>	/	No conv.**	/	/

Moonlight *	Relative abundance		TMedianP1	
	Gestation	Lactation	Gestation	Lactation
<i>E. serotinus</i>	-0.21	0.11	-478.66	-118.01
<i>M. daubentonii</i>	/	/	/	/
<i>N. leisleri</i>	-0.10	/	335.96	322.38
<i>N. noctula</i>	/	/	256.78	504.30
<i>P. kuhlii</i>	/	/	/	77.01
<i>P. nathusii</i>	-0.13	/	249.54	/
<i>P. pipistrellus</i>	/	/	/	138.84
<i>P. pygmaeus</i>	-0.20	No conv.**	/	/

Artificialized surfaces *	Relative abundance		TMedianP1	
	Gestation	Lactation	Gestation	Lactation
<i>E. serotinus</i>	/	/	/	/
<i>M. daubentonii</i>	-1.38	/	/	332.82
<i>N. leisleri</i>	0.18	/	/	/
<i>N. noctula</i>	0.63	0.65	/	/
<i>P. kuhlii</i>	0.43	0.45	/	/
<i>P. nathusii</i>	0.24	0.32	/	396.65
<i>P. pipistrellus</i>	/	/	/	/
<i>P. pygmaeus</i>	0.57	No conv.**	/	/

* These results are only preliminary as, despite our precautions, (1) some temporal and/or spatial autocollinearity remain for some species, (2) first checking of model assumptions with the package DHARMA also showed that some assumptions could have been violated for some species.

** For *P. pygmaeus*, for the relative abundance and during lactation, some models in the dredge did not converge.

Box 6: Impact of light pollution on the abundance and timing of activity of open- and edge-space-foraging bat species at landscape scale (in prep)

4



emergence when light levels are relatively high. Conversely, during lactation high energetic needs might lead bats to take risks even if light levels are relatively high. For *M. daubentonii* and *P. nathusii* artificialized surfaces were selected over ALAN.

We found that **moonlight** affected the timing of activity of many species. Surprisingly, for *E. serotinus*, we found that moonlight made activity earlier, contrary to what we found in Mariton et al. (2022). Such result will need to be explored. For the other species, when moonlight impacted the timing of activity, it was always to delay it. Interestingly, while the effect of moonlight occurred during at least gestation for the two *Nyctalus* and *P. nathusii*, for *P. kuhlii* and *P. pipistrellus* this delaying effect was only found for lactation. This might suggest that the effect of moonlight on bat timing of activity might not only be driven by a trade-off between predation risks and energetic needs, but also, by other mechanisms that we will have to explore.

Overall, these preliminary results suggest that open- and edge-space-foraging bat species might **not really be “light tolerant”**. For four of the species studied we found that ALAN negatively affected their abundance and/or delayed their timing of activity during gestation and/or lactation. For the other four species, the absence of response to light pollution should be considered with caution. Indeed, they might not be impacted by ALAN, however, they might also not be able to adapt the choice of their foraging sites or their timing of activity to the presence of ALAN. Considering our results in the light of the specialisation of these eight species to given habitats or diets could therefore be a future perspective.

Chapter 3: Are technological developments in lighting threats to bats?

“Lights, lights, lights sparkled everywhere! The lights were many coloured and all were mirrored in the wet tarmac.”

Suzanna Clarke, Piranesi

Based on the publication:

Kerbiriou, C., Barré, K., **Mariton, L.**, Pauwels, J., Zissis, G., Robert, A., Le Viol, I., 2020. Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of Bats. Diversity 12, 165. <https://doi.org/10.3390/d12040165>



Figure 24: Hypotheses of Kerbiriou et al., (2020)

Context

Once the use of ALAN has been restricted to areas and times when it cannot be switched off, three main levers should still be considered to reduce light pollution: reducing light trespass, reducing light intensity and choosing a light source whose spectrum of emission is the least detrimental for biodiversity. The phase-out and replacement of old lighting equipment in developed countries could be an opportunity to implement these three mitigation measures.

In particular, LEDs are widely used for new lighting equipment and for retrofitting old equipment. As this lighting technology have a high luminous efficacy (i.e. a measure of how well a light produces visible light, see **Box 1**), it has the potential to reduce expenditure and CO₂ emissions associated with ALAN (Kyba, 2018; Sánchez de Miguel et al., 2022; Stone et al., 2012). However, warnings have been raised about a possible “rebound effect”, that is to say that this efficacy is more likely to results in increased use of light as it becomes cheaper rather than in reduced energy consumption (Kyba, 2018; Sánchez de Miguel et al., 2022).

Furthermore, because LEDs have a broad emission spectrum (**Figure 3**), they can trigger a wide range of wavelength-specific biological responses. LEDs therefore have the potential to disrupt many biological processes and organisms (Sánchez de Miguel et al., 2022). In particular, most LEDs used in outdoor lighting are rich in blue light (Kyba, 2018), to which many biological responses have been shown to be sensitive (Sánchez de Miguel et al., 2022). For instance, terrestrial invertebrates have been shown to be more attracted by light sources emitting a high proportion of short-wavelengths (e.g. Bolliger et al., 2022; Lockett et al., 2021; Pawson and Bader, 2014; Somers-Yeates et al., 2013), with potential cascading effects on their predators. Assessing the effect of replacing of old lighting technologies with LEDs on biodiversity should therefore be an urgent concern.

McNaughton et al. (2021) found that a switch from HPS lamps to LEDs resulted in alterations of the timing of dawn song in birds, modifications in the avian community composition, an increase in avian species richness and an increase in ground insect activity. Likewise, Pawson and Bader (2014) found that LED light traps captured more insects than light traps fitted with HPS lamps. While some studies have shown a repulsive or attractive effect of LED lights on bats compared to dark sites (Rowse et al., 2018; Russo et al., 2019; Seewagen and Adams, 2021; Stone et al., 2012), to date, very few studies have focused on the impact of switching from old lighting technologies to LEDs on bats. Haddock et al. (2019) found that the activity of some bat species, in Australia, decreased when MV lamps were replaced by LEDs. MV lamps have the particularity of having a peak of emission in the

ultraviolet (**Figure 3**), so they are likely to attract even more insects than LEDs, and thus be more attractive to “light-tolerant” bat species. Rowse et al. (2016) is the only study that focused on a type of lamp that was widely used in Europe, LPS lamps, which emit a narrow-band spectrum with a single energy peak in the yellow range (**Figure 3**). They found that switching from LPS lamps to LEDs had no impact on bat activity.

However, when old lighting equipment are replaced, the emission spectrum is usually not the only characteristic of lamps that changes. For instance, Rowse et al. (2016) noted that illuminance and power were modified during the real-life replacement they studied. Such a modification should not be overlooked as bat responses to light pollution has been shown to depend on light intensity. At the local scale, it has been shown the activity of narrow-space-foraging species (i.e. “light intolerant” species) was negatively affected by illuminance regardless to the emission spectrum of the lamps (HPS: Azam et al., 2018, LPS and MV: Lacoëuilhe et al., 2014, LED: Rowse et al., 2018), and even at low light levels (Azam et al., 2018; Lacoëuilhe et al., 2014). For the open- and edge-space-foraging species, which are usually considered to be “light tolerant”, illuminance has also been shown to affect their activity, however results vary according to the species and lamp types. Overall, at the local scale, illuminance seems to have a positive effect on the activity of some of these species (HPS: Azam et al., 2018, LPS and MV: Lacoëuilhe et al., 2014, MV and LED: Lewanzik and Voigt, 2017, LED: Rowse et al., 2018). However, Azam et al. (2018) found a mixed effect of illuminance on *E. serotinus*, and they showed that, for *P. pipistrellus* and *N. leisleri*, the positive effect of illuminance peaked between 1 and 5 lx and then decreased. Lacoëuilhe et al. (2014) even found a negative effect of illuminance of *N. leisleri* and Hale et al. (2015) showed that the barrier effect of ALAN on *P. Pipistrellus* was stronger with increasing illuminance. Similarly, the studies presented in the second chapter of this PhD suggest that, at the landscape scale, even species usually considered to be light tolerant, may be sensitive to low light levels (Mariton et al., (2022) and **Box 6**). Therefore, when studying the replacement of old lighting equipment with new, it is necessary to take into account not only the change in the emission spectrum but also the changes in intensity.

Prior to 2020, Rowse et al. (2016) was the only study to investigate the switch from the widely used LPS lamps to LEDs. The dataset they used in this study was very valuable as it was based on a before-after-control-impact paired (BACIP) design on 12 sites in four counties across southern England. They focused on “real-life” switches in lighting technologies by local authorities and they took care to record bat activity at least seven days after the switch-over, to allow bats to adjust to the characteristics of the new lights. We therefore believed that it was

of utmost interest to try to disentangle the relative effects of the emission spectrum from the effects of illuminance or power in their study. Thus, we conducted a retrospective analysis of their data to include these covariates in statistical models. We intended to answer the following questions:

(1) Does the switch from LPS lamps to LEDs impact bat activity?

We hypothesised that since LEDs emit a greater amount of short wavelengths than LPS lamps, the switch from LPS lamps to LEDs would lead to an increase in the number of insects attracted to the streetlights and thus result in an increase in the activity of “light tolerant” species (**Figure 24**).

(2) Is bat activity influenced by the interaction between light intensity and emission spectrum?

We hypothesised that light intensity would influence bat activity according to a trade-off between the opportunity to exploit the insect biomass around streetlights and a perception of increased predation risks when exposed to light. Their responses to light intensity could then vary according to the emission spectrum. Indeed, because LED light is closer to daylight characteristics than the light emitted by LPS lamps, an increase in light intensity under LED lamps could lead to greater perception of the potential risk of predation exposure than under LPS lamps. We thus hypothesised that bat activity would increase under LED lamps when light intensities were low, whereas it would decrease under high light intensities (**Figure 24**).

Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of Bats

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Abstract (Figure 25)

Artificial light at night is considered a major threat to biodiversity, especially for nocturnal species, as it reduces habitat availability, quality, and functionality. Since the recent evolution in light technologies in improving luminous efficacy, developed countries are experiencing a renewal of their lighting equipment that reaches its end-of-life, from conventional lighting technologies to light emitting diodes (LEDs). Despite potential cascading impacts of such a shift on nocturnal fauna, few studies have so far dealt with the impact of the renewal of street lighting by new technologies. Specifically, only one study, by Rowse et al. 2016, examined the effects of switching from widely used low pressure sodium (LPS) lamps to LEDs, using bats as biological models. This study was based on a before-after-control-impact paired design (BACIP) at 12 pairs in the UK, each including one control and one experimental streetlight. If Rowse et al. 2016 showed no effect of switching to LEDs streetlights on bat activity, the effects of respective changes in light intensity and spectrum were not disentangled when testing switch effects. Here, we conduct a retrospective analysis of their data to include these covariates in

statistical models with the aim of disentangling the relative effects of these light characteristics. Our re-analysis clearly indicates that the switches in spectrum and in intensity with replacement of LPS with LED lamps have significant additive and interactive effects, on bat activity. We also show that bat activity and buzz ratio decrease with increasing LED intensity while an opposite effect is observed with LPS lamps. Hence, the loss or the gain in bat activity when lamp types, i.e., spectrum, are switched strongly depends on the initial and new lamp intensities. Our results stress the need to consider simultaneously the effects of changes in the different lights characteristics when street lighting changes. Because switches from LPS to LED lamps can lead to an increase in light intensity, such technological changes may involve a reduction of bat activity in numerous cases, especially at high LED intensities. Since we are currently at an important crossroad in lighting management, we recommend to limit LED intensity and improve its spectral composition toward warmer colors to limit potential deleterious impacts on bat activity.

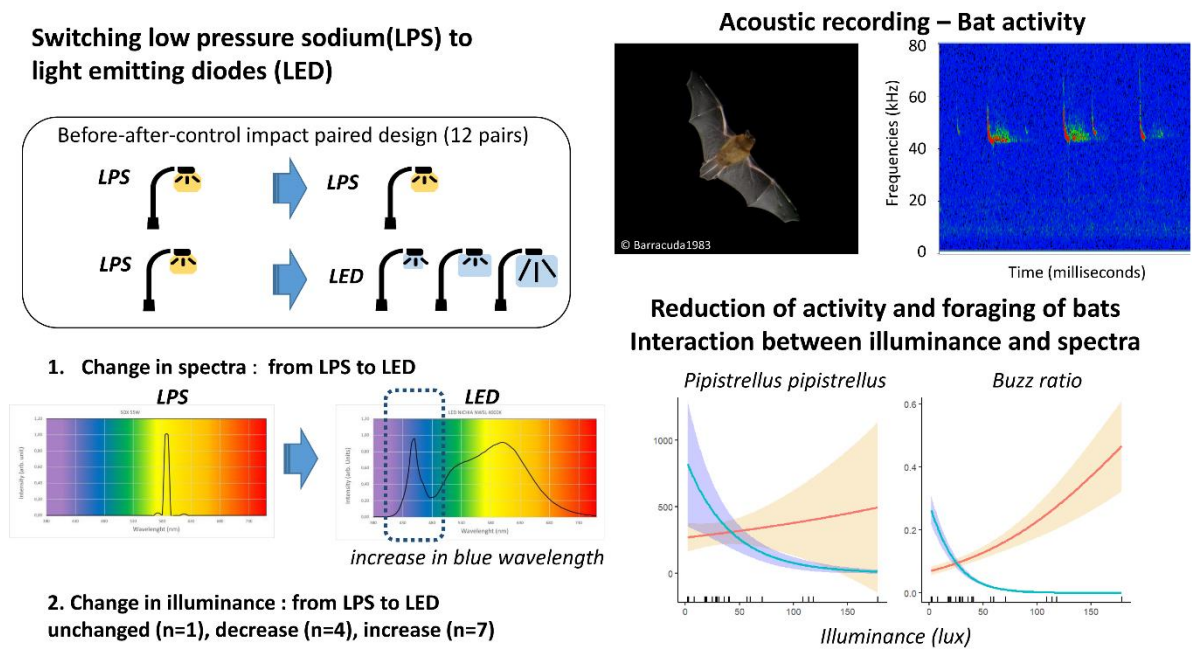


Figure 25: Graphical abstract of Kerbiriou et al. (2020)

Keywords: artificial light at night; light pollution; bat activity; LED streetlight; Chiroptera

1. Introduction

Light pollution induced by the widespread use of artificial light at night (ALAN) is a global pressure on the ecosystem, affecting 23% of the global land surface (88% of Europe [1]) and expanding at an annual rate of 6% worldwide [2]. As ALAN alters the natural periodicity of day and night, it can disrupt the circadian and seasonal rhythms of both diurnal and nocturnal species. This pressure can affect individual fitness, sexual selection, and reproductive success [3,4,5]. In addition, species responses to ALAN are driven by repulsion/attraction behaviors, thereby artificial lighting can alter the movement and distribution of species at multiple spatial scales [6,7,8,9]. Taken together, ALAN effects can dramatically affect biological communities [10,11] and ecosystem functions [12].

ALAN also consumes 19% of total global electricity and accounts for 1900 Mt of CO₂ emissions per year [2]. Thus, a current major challenge in land-use planning involves designing outdoor lighting strategies that save energy and reduce CO₂ emissions while limiting negative effects on biodiversity [2]. In the European Union, the most widely used streetlamp types are sodium vapor lamps (high pressure sodium, HPS and low pressure sodium, LPS), metal halide (MH), and high pressure mercury vapor lamps (HPM), representing respectively 37%, 36%, and 27% sales for the period 2004–2007 [13]. However, since the European Eco-Design Directive (245/2009), and according to the recent evolution of light technologies, developed countries are experiencing a renewal of their lighting equipment that reaches its end-of-life, from conventional lighting technologies to light emitting diodes (LEDs) [14]. Specifically, LEDs have a high luminous efficacy (i.e., amount of energy needed to produce visible light in lumen per watt), and thus offer great opportunities to save energy and limit CO₂ emissions [15]. In addition, conventional lighting technologies are being progressively phased out from the market because of their lower energetic efficiency [13]. This change is occurring concomitantly with the increasing cost-effectiveness of energy-efficient LEDs, representing so far approximately 7% of the European market [16]. This “breakthrough” lighting technology is an opportunity to drastically reduce the energy consumption of lighting compared to existing conventional lighting technologies, while allowing a greater flexibility in the control of the light environment as well as reducing maintenance costs [14]. However, this technology shift is accompanied by a change in light intensity and spectrum [14,17]. Indeed, both warm and cold white LEDs (2700 K and 4000 K, respectively) present an important peak of emissions in blue and ultraviolet (UV) wavelengths, which induces physiological disruption affecting animals [18,19,20], and is responsible for the flight-to-light behavior of insects [21].

Thus, the expected massive deployment of this technology in public outdoor lighting raises major concerns regarding its potential impacts on biodiversity.

Strictly nocturnal animals such as microchiropteran bats are particularly likely to be affected by ALAN, since they may be exposed to it during their entire activity period. In addition, microchiropteran bats present contrasting responses to ALAN according to their flight abilities and foraging strategies [22]. While slow-flying gleaner bat species avoid illuminated areas [9,23], common fast-flying aerial and hawking species such as *Pipistrellus* spp. forage for insects in open areas and are able to forage at the vicinity of streetlights that provide a more predictable insect biomass [22,23,24]. It is known that HPS lights attract moths, because of the presence of UV wavelengths (**Figure 26**), while LPS lights of the same intensity (not producing UV light) attract less moths [25]. Such differences in bat prey attractiveness impact in turn bat behavior. However, bats also have to deal with a trade-off that includes the benefits of foraging close to streetlights and the drawback of increased predation risk by exposure to light [26]. Such a trade-off can also induce a light avoidance behavior, which was detected regardless of the lamp spectrum [27] and even at low level of light illuminance [24,28]. In this context, we hypothesize that a switch from conventional lighting technologies to LEDs may produce contrasted effects on moth attraction and in turn on predators such as fast-flying bat species. Thus, the consequences of a renewal of street lighting on bat depend on changes in spectral composition and changes in the various components of light intensity (here, two aspects of intensity are considered: power (watts) and illuminance (lux), see **Supplementary Material 1**), it is thus not trivial to predict whether the renewal will conduct to an increase or a decrease in bat activity under streetlights. Thus, the consequences of a renewal of street lighting on bat depend on changes in spectral composition and changes in the various components of light intensity (here, two aspects of intensity are considered: power (watts) and illuminance (lux), see **Supplementary Material 1**), it is thus not trivial to predict whether the renewal will conduct to an increase or a decrease in bat activity under streetlights.

This renewal of street lighting by new technologies is happening worldwide. However, despite its potential cascading impacts on nocturnal fauna, few studies have so far dealt with the impacts of such a shift. Due to the lack of published studies, conducting a meta-analysis on this issue is not an option nowadays. Hence, all published works get close attention and the message conveyed can be viewed as a direct example to follow. In this context, Rowse et al. [17] set up one of the first in situ experiments to investigate the effect of a switch from commonly used LPS to LED lamps on microchiropteran bat activity. LPS and LED lamps are

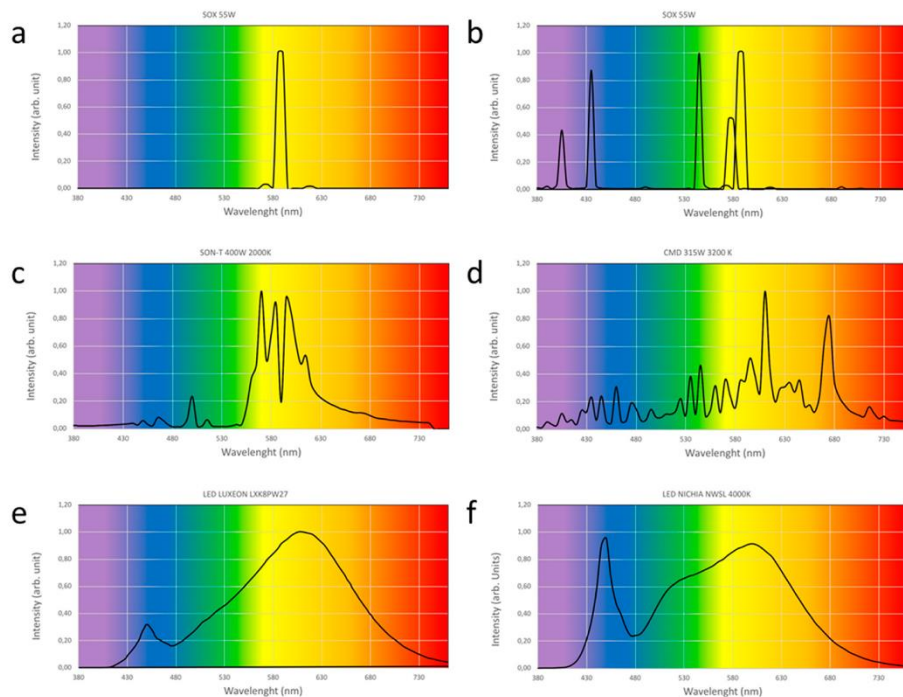


Figure 26 : Spectra (visible domain 360–780 nm) of some commonly used lamps for outdoor lighting systems. Luminous intensities are normalized to the maximum value: **(a)** low pressure sodium (LPS) lamp (under ban due to eco-conception rules); **(b)** mercury high pressure lamp (MV) (under ban); **(c)** high pressure sodium lamp (HPS); **(d)** ceramic metal halide lamp (MH); **(e)** warm white light emitting diodes (LED) (2700 K); **(f)** cool white LED (4000 K). Spectral data are measured by LAPLACE laboratory (private communication).

in that case, as in common practices (i.e., common sense for practitioners), mainly distinguished according to the most important change in their characteristics, i.e., in their spectrum. LPS lamps emit narrow-band spectrum with a single peak of energy in the yellow range (~ 1807 K, **Figure 26a**), while LEDs used in this experiment were cool and neutral white emitting lamps (4000–5700 K), with a significant peak of blue emissions (**Figure 26e,f**). Thus, as insects are more attracted to short wavelengths such as blue and UVs than longer wavelengths such as yellow [21], it would be expected to find a positive effect of a switch from LPS to LEDs on the foraging activity of so-called “light-attracted” fast-flying species. To test this hypothesis, the authors of this study did a before-after-control impact paired design (BACIP) at 12 pairs in four UK counties. Each pair consisted in two sites of existing streetlights, with one control site remaining LPS throughout the study, and one experimental site switching from LPS to LED ([17] for complete description of the experiment). One of the strengths of this study lies in the fact that the authors monitored the effect of a real-life switch from LPS to LED streetlights performed by local authorities. Thus, their experiment corresponded to both ecological and public lighting realities. However, they did not control for

lamp parameters that could potentially act as confounding effects in their study. In particular, although they intended to pair control and experimental streetlights at each site with similar height (m), and with similar lamp characteristics: light intensity (two metrics: output power (watts) and illuminance received by horizontal surface (lux)), there were still drastic differences in light illuminance and power output between the LPS lamps and the LEDs they were replaced by. It is, however, well known that light intensity is an important factor that can influence bat activity [24,28].

In their study, Rowse et al. [17] did not detect any effect of the switch from LPS to LED lamps on bat activity. However, as several light intensity characteristics (i.e., power and illuminance) changed between the “before” and “after” phases, we believe it is necessary to include the influence of those characteristics in statistical models. In addition, we also believe that using generalized linear mixed-effects models (GLMMs) is a more robust approach than the non-parametric approaches used by Rowse et al. [17] because GLMMs can directly use the information of bat activity abundance (i.e., the response variable) through error distribution adapted for count data with potential over-dispersion [29]. Hence, we conducted a retrospective analysis of Rowse et al.’s data [17] using an alternative approach aiming at disentangling the relative effects of light spectrum and intensity (i.e., power and illuminance) on bat activity following a switch from LPS to LED lamps.

According to the changes in spectrum composition, the switch from LPS to LED lamps will increase the amount of short wavelengths, and in return, contribute to attract much more insects [30]. We thus hypothesize that it will increase the activity of light-tolerant bats. However, bats are also sensitive to light intensity [28] due to the potential risk of predation exposure [31,32]. In this context, we expect that differences in bat activity generated by the switch from LPS to LED lamps will also depend on light intensity. In addition, LED light being closer to daylight characteristics, the increase in light intensity under LED lamps could lead to greater perception of the potential risk of predation exposure than LPS. The net result on bat activity (increase or decrease) will depend on a trade-off between the risk of predation exposure and the increase in prey resource. Therefore, we hypothesize that bat activity will increase under LED lamps when light intensities are low, while it would decrease under high light intensities.

2. Material and Methods

2.1. Biological Model

Bats are increasingly threatened worldwide [33]. At the very local scale (i.e., the streetlight scale), some bats are able to feed on moths and flies attracted by streetlamps, these species named “light-tolerant species” are mainly fast-flying aerial hawking species (i.e., those in the genera *Eptesicus*, *Nyctalus*, and *Pipistrellus*). These species may benefit locally from the amount of prey [22]. In contrast, some species systematically avoid lit areas when commuting [8] and foraging [22]. These species, considered as “light-intolerant species”, mainly include slow-flying bat species that avoid open areas such as *Myotis spp.* and *Rhinolophus spp.* Thus, artificial light may potentially intensify “interspecific competition for food” between rare species such as *R. hipposideros* and common species such as *P. pipistrellus* [34].

2.2. Bat Activity

According to their foraging strategy during the reproduction period, (i.e., individuals foraging around maternity roost [35,36] using commuting corridors), the assessment of impact of anthropogenic pressures on bat relative abundance should favor in situ experiments that take into account landscape constraints. Acoustic recorders that allow users to measure bat activity, often considered as a proxy of relative abundance, were hence increasingly used over the last two decades in such studies, to test various anthropogenic pressures including artificial light at night at local scales [8,23,37]. Here, the proxy of bat activity was the number of bat passes over three consecutive nights [17]. Because bat passes were not detailed for each night, this group of three consecutive nights referred to a categorical variable hereafter named “date”. This measure of bat passes allowed deriving five bat activity measures: the total number of bat passes, the number of bat passes for a given species (*P. pipistrellus*, *P. pygmaeus*, and *Nyctalus spp.*) and the feeding buzz ratio of *P. pipistrellus*. Before catching an insect, bats produce particular echolocation calls, named buzzes [38]. The buzz ratio (i.e., the proportion of bat passes that included feeding buzzes) can reveal substantial information about capture success and can be used as an indirect proxy of bat’s prey density [39].

2.3. Experimental Set-up and Variation in Power and Illuminance of Lamps at Experimental Sites

In order to investigate the impact of a switch from LPS to LED streetlights on bat activity, Rowse et al. [17] performed a before-after-control-impact paired design (BACIP), at 12 pairs across southern England. Each pair include one experimental lighting column (switch from LPS to LED) and one control lighting column (remaining LPS throughout the study). Control lighting columns (hereafter named control) were selected in landscapes where LPS lights remained the dominant lighting type throughout the study. Experimental lighting columns (hereafter named experimental) were selected in landscapes where LPS lights were the dominant lighting type before the switch-over and where LED were the dominant lighting type after the switch-over (for more details on the characteristics of sampled lighting columns see [17]). The LED lamps (hereafter name LED) studied were a combination of neutral and cool LED lights (4000–5700 K, see **Figure 26e,f** for spectrum composition). An exploration of landscape composition and streetlight column characteristics among sites using principal correspondence analysis confirmed the absence of the site with an obvious peculiar composition (see **Supplementary Material 2**)

Because bat activity measure is linked to prey invertebrate availability, and in turn, weather conditions [40,41,42], weather conditions have to be consequently taken into account in the design of in situ experiments. In order to disentangle the effects of a switch from LPS to LED on bat activity from the effects of weather conditions, Rowse et al. [17] sampled the two recording sites of a pair (treatment and control) during the same night. Recordings were made a minimum of seven days (mean 14.9 days, s.d. ± 5.3 days) after the switch-over, with the aim to enable the bats to adjust to the new lights [17].

Table 3: Variations in power and illuminance at Rowse et al.'s study.

Variations were computed as the differences between the power/illuminance of low pressure sodium (LPS) in experimental before the switch-over and the power/illuminance of LED after the switch-over.

Light intensity	Mean (\pm SE)	Minimum	Maximum
Changes of power (watts)	-10.6 ± 3.8 (-40%)	-21 (-61%)	+16 (+18%)
Changes of illuminance (lux)	$+17.7 \pm 8.5$ (+259%)	-21 (-51%)	+64 (+1800%)

As Rowse et al. [17] worked on the switch of streetlights from LPS to LED performed by local authorities, they could not define themselves (i) the date of switch-over, thus leading to a staggering of the recording period from May to October 2014; and (ii) the new lamp characteristics. Concerning the first point, the staggering of the recording period from May to October is not an optimal sampling because bat activity changes dramatically during this timeframe [43]. Concerning the second point regarding new lamp characteristics, it is much more problematic, because, in addition to change in spectrum, the switch from LPS to LED resulted in drastic changes in light intensity (power and illuminance) of streetlamps (**Table 3**).

Consequently, we believe it is important to disentangle the effects of changes in these characteristics (illuminance and power) from changes in lamp type (spectrum) on bat activity to fully assess the effects of switching from LPS to LED.

2.4. Statistical Analyses

2.4.1. Preliminary Analysis 1: Analysis without Taking Account Changes in Light Intensity (Power and Illuminance)

Since we changed the conceptual framework of statistics (from non-parametric test to generalized linear modeling), firstly we performed similar analysis as Rowse et al. [17] (i.e., without taking into account changes in light intensity). Using the generalized linear mixed-effects model (GLMM; function and R package glmmTMB [44]), we also found qualitatively similar results as Rowse et al. [17] found using non-parametric tests, except for buzz ratio: our modeling allowed detecting a significant decrease in buzz ratio associated with the switch from LPS to LED occurring (see details in **Supplementary Material 3**).

2.4.2. Preliminary Analysis 2: Evaluation of the Influence of Intensity (Power and Illuminance) on Bats Activity

We assessed the relative importance of illuminance and power variables on bat activity compared to other explanatory variables (height, dist. wood, dist. water, dist. grass) using generalized linear modeling or hierarchical partition of the variance applied on the Rowse et al.'s dataset [17]. We confirmed the correlation between bat activity and power and illuminance (see **Supplementary Material 4**).

2.4.3. *Disentangling the Relative Effects of Light Spectrum and Intensity (i.e., Power and Illuminance) on Bat Activity Following the Switch from LPS to LED Lamps*

According to the two preliminary findings, i.e., (i) the correlation between bat activity and power and illuminance, which is congruent with the literature [24,28]; and (ii) the changes in power and illuminance between the before and after stages for experimental lighting columns (**Table 3**), we believe that including illuminance and power covariates in the statistical analyses is necessary to assess the effects of the lamp type per se (LPS and LED, i.e., major changes in spectrum) on bat activity. When reanalyzing data, we performed GLMM using as response variable of the number of bat passes, as explanatory variables of the lamp type (LPS versus LED) and the intensity (power or illuminance) as well as the interaction between lamp type and illuminance or power. In addition, we used a nested random effect (date within pairs) to account for the structure of the data (each site, i.e., a pair, consisted of a control and an experimental recording site sampled the same date before and the same date after). It should be noted that date was a categorical variable used to group data recorded on the same date, but was not informative as to the actual date of sampling. Because power and illuminance were obviously correlated (Spearman's $\rho = 0.64$, [45]), we performed independent modelings: one included power while the second included illuminance. According to the nature of the response variable (count of bat passes) and potential over-dispersion, we performed modelings using a negative binomial distribution (link = log) [29], except for feeding buzz ratios, for which we used a binomial distribution (link = logit). Thus, our statistical models were structured as follows:

$$\text{Bat Activity} \sim \text{Lamp Intensity} \times \text{Lamp Type} + (1|\text{Pair/Date}) \quad (1)$$

where Bat activity was (i) the number of passes for a given species, (ii) the feeding buzz ratio or (iii) a total number of bat passes, Lamp intensity was either the power or the illuminance variable and Lamp type referred to the spectrum (LPS or LED).

It is worth noting that in the data of Rowse et al. [17], bat activity may have been strongly influenced by the season (from May to October), which may have generated a high degree of heterogeneity in the results. However, the paired experimental design and the structure of the statistical model (random “pair” effect) make it possible to incorporate this variation without compromising the statistical power of the tests because the two measurements from the same pair (control and experimental sites) were always spatially close and were recorded simultaneously.

A total bat activity could be strongly driven by species identity (because of differences of local abundances between species or specific distances of detection [46], some species can have more weight than another can). Instead of summing the activity of the different species, we thus added a nested random effect on the species to all models with *total number of bat passes* as the response variable. Finally, we checked for over-dispersion and for homogeneity of variance by visual inspection of residuals [47].

3. Results

When the lamp type effect was modeled using power as the covariate, we found that LED lamps increased the total bat activity, the *Nyctalus spp.* activity, and the buzz ratio as compared to LPS. Overall, power has a negative effect on *Pipistrellus pipistrellus* activity and buzz ratio (**Table 4**). The relationship between bat activity and power significantly differed between LPS and LED lamps for total bat activity, the buzz ratio, and species activity measures except for *Pipistrellus pygmaeus*. Specifically, increasing power tended to increase bat activity with LPS lamps, while it tended to decrease bat activity with LED lamps (**Table 4; Figure 27**).

When the lamp type effect was modeled using illuminance as the covariate, we found that LED lamps increased buzz ratio and activity of *P. pipistrellus* as compared to LPS. Overall, like power, the illuminance has a negative effect on *P. pipistrellus* activity and the buzz ratio (**Table 4**). The relationship between bat activity and illuminance significantly differed between LPS and LED lights for total bat activity, the buzz ratio, and species activity except for *P. pygmaeus* as well. As in the power analysis, increasing illuminance increased bat activity with LPS lamps, while it decreased it with LED lamps (**Table 4; Figure 28**).

4. Discussion

In contrast to the study of Rowse et al. [17], which concluded that the switch from LPS to LED lamps had no effect on bats, our analyses indicate that the switch from LPS to LED lamps (i.e., in spectrum) has a significant effect on bat activity, although this effect strongly depends on light intensity level. The main reason for such discrepancy between our conclusion and that of Rowse et al. (2016) comes from the inclusion of changes in light intensity in our statistical modeling. The loss or gain in activity that results from this switch in spectrum

Table 4: Effects of the type of lamp (LPS versus LED), the lamp intensity (illuminance or power), and their interaction on bat activity.

The estimates of LampLPS are the difference in bat activity between LPS lights and LED lights placed as intercept (i.e., a negative estimate indicates that bat activity is lower with LPS compared to LED for a given light intensity). The estimates of the interaction (LampLPS:Lamp intensity) correspond to the difference of slope between the two regressions (bat activity ~ Lamp intensity) according to the lamp type (i.e., LPS versus LED).

	Illuminance		Power	
	Estimate ± SE	P-value	Estimate ± SE	P-value
<i>Total bat activity</i>				
Intercept	3.670 ± 0.917	<0.001	3.713 ± 0.898	<0.001
LampLPS	-0.733 ± 0.393	0.062	-0.988 ± 0.456	0.030
Lamp intensity	0.001 ± 0.007	0.896	0.001 ± 0.010	0.945
LampLPS:Lamp intensity	0.021 ± 0.007	0.003	0.022 ± 0.010	0.029
<i>Pipistrellus pipistrellus</i>				
Intercept	6.760 ± 0.586	<0.001	6.584 ± 0.522	<0.001
LampLPS	-1.168 ± 0.566	0.039	-0.732 ± 0.625	0.241
Lamp intensity	-0.024 ± 0.009	0.005	-0.033 ± 0.012	0.004
LampLPS:Lamp intensity	0.027 ± 0.010	0.008	0.030 ± 0.014	0.033
<i>Pipistrellus pygmaeus</i>				
Intercept	2.180 ± 0.935	0.020	2.578 ± 0.799	0.001
LampLPS	-0.318 ± 0.922	0.730	-1.248 ± 0.918	0.174
Lamp intensity	0.027 ± 0.015	0.080	0.031 ± 0.016	0.052
LampLPS:Lamp intensity	-0.001 ± 0.017	0.968	0.003 ± 0.018	0.886
<i>Nyctalus spp.</i>				
Intercept	2.093 ± 0.786	0.008	2.335 ± 0.808	0.004
LampLPS	-0.773 ± 0.547	0.158	-1.578 ± 0.712	0.027
Lamp intensity	-0.001 ± 0.010	0.886	-0.014 ± 0.017	0.403
LampLPS:Lamp intensity	0.032 ± 0.009	0.001	0.051 ± 0.014	<0.001
<i>Feeding buzz ratio</i>				
Intercept	-0.931 ± 0.237	<0.001	-0.662 ± 0.262	0.012
LampLPS	-1.681 ± 0.188	<0.001	-2.415 ± 0.294	<0.001
Lamp intensity	-0.052 ± 0.004	<0.001	-0.132 ± 0.009	<0.001
LampLPS:Lamp intensity	0.066 ± 0.004	<0.001	0.154 ± 0.010	<0.001

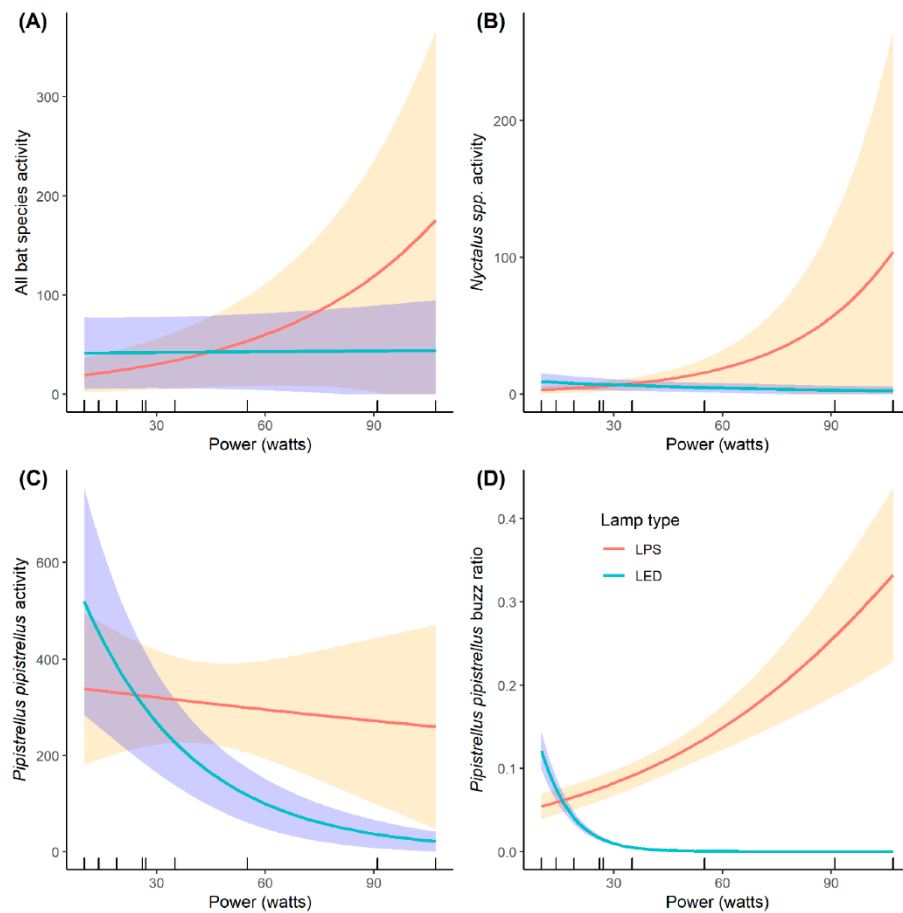


Figure 27 : Predicted bat activity as a function of the light power according to the lamp type (light emitting diodes (LED) and low pressure sodium (LPS)) (total bat activity (A), *Nyctalus* spp. Activity (B), *Pipistrellus pipistrellus* activity (C) and *P. pipistrellus* buzz ratio (D)). Results come from interactions presented in the light power modeling (right side of **Table 4**).

strongly depends on both initial and new lamp intensities: at the lowest intensities, bat activities were higher near LED than LPS, while for high intensities it was the opposite (i.e., bat activity and buzz ratio decrease with increasing LED intensity, while an opposite effect was observed with LPS lamps). Because switches from LPS to LED lamps can lead to an increase in illuminance, these results indicate that such technological changes may involve a reduction of bat activity in numerous cases, especially at high LED intensities.

According to the limited number of sites sampled, these results should be treated with caution and we encourage repeating such study. In addition, these results should also be used with caution as they are based on whole-night activity metrics, which do not provide information on the full range of possible impacts. Indeed, artificial light also disrupts the behavior, phenology, and physiology of individuals [48,49,50], which should be assessed with

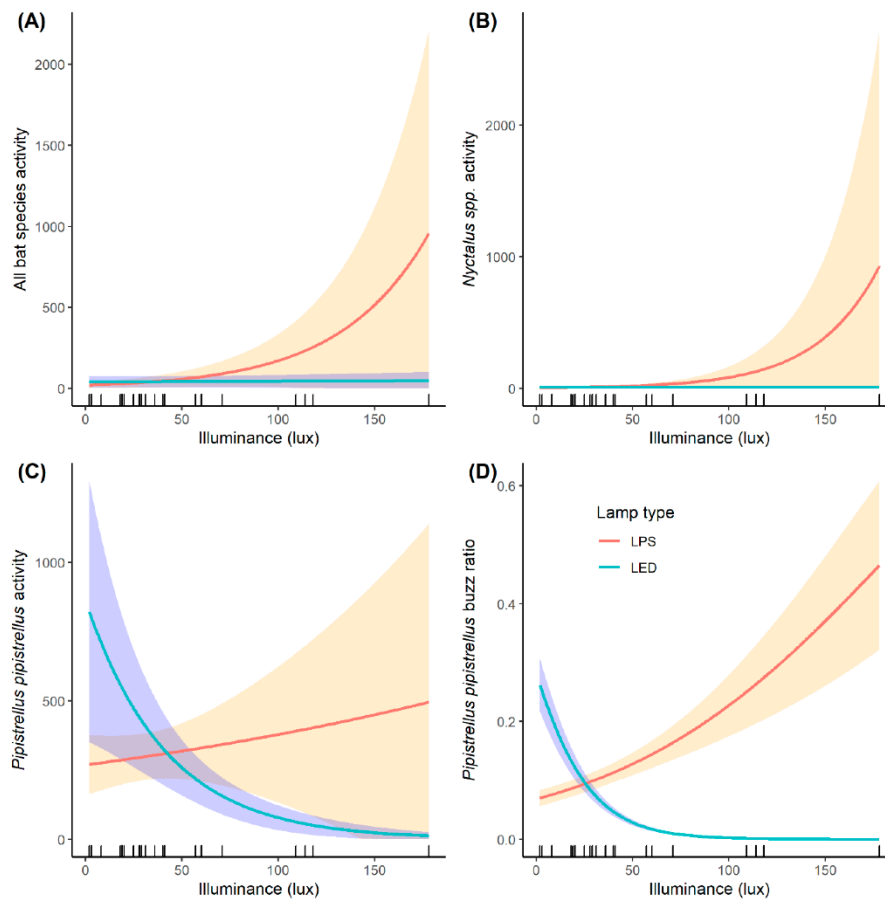


Figure 28: Predicted bat activity as a function of the light illuminance according to the lamp type (light emitting diodes (LED) and low pressure sodium (LPS)) (total bat activity (A), *Nyctalus* spp. Activity (B), *Pipistrellus pipistrellus* activity (C) and *P. pipistrellus* buzz ratio (D)). Results come from interactions presented in the light illuminance modeling (left side of **Table 4**).

phenology, and physiology of individuals [48,49,50], which should be assessed with more accurate temporal resolution. Unfortunately, this information was not available.

The interaction between spectrum and intensity reveals a trade-off between foraging opportunities and risks of exposure to predation when bats forage in a lit environment. On one hand, streetlight made up of lamp types with important proportion of blue or UV wavelengths (cool white LED, HPM, MH, **Figure 26**), concentrate insects' preys [33] and therefore can be attractive for light tolerant bat species, but on the other hand, the increase of intensity may be perceived as an increase of the risk of exposure to predation [33,34]. Thus, the trade-off between the increase in prey amount and the increase of predation risk, both linked to the increase in light intensity, appears to be more profitable for bats under LPS than LED lamps. An assumption to explain this difference is that LED light is closer to daylight characteristics and is thus associated to a greater risk of predation exposure. Our results also confirmed the

hypothesis that at low intensity, the direction of the effect of change in spectrum on bat activity—of light-tolerant bats—should depend on the amount of UV and of blue wavelengths as these parameters induce more phototaxis of flying insects [21]. At the lowest intensities, the switch from LPS to LED and hence the increase in amount of UV and of blue wavelengths, resulted indeed in an increase of bat activity. This result is also congruent with the study performed by Stone et al. [51] on the impact of the switch from LPS to white metal halid lamps. Such change resulted in an increase in the amount of UV and blue wavelengths emitted (**Figure 26d**) and led to an increase of light-tolerant bat activity (*Pipistrellus pipistrellus*, *P. pygmaeus*, and *Nyctalus/Eptesicus* spp.) [51]. In contrast, a decrease of light-tolerant bat activity should be expected for a switch from mercury vapor (MV) to LED lamps, because it will contribute to a decrease of the amount of UV and of blue wavelengths emitted (LED includes a lower amount of wavelengths attractive for insects (**Figure 26e,f** for LED compared to **Figure 26b** for MV)). This result was found by Lewanzik and Voigt [52] who detected a decrease in bat activity when mercury vapor (MV) lamps were switched to LED lamps.

However, the observed increase or decrease in bat activity under streetlights consecutively to the renewal of conventional lights to LED should be carefully interpreted. Firstly, whatever the type of spectrum or light intensity, some bats species systematically avoid lit environments, particularly slow-flying species adapted to prey on insects in cluttered vegetation, such as *Rhinolophus* spp. and *Myotis* spp. [8,9,23]. Secondly, even for light tolerant species such as *Pipistrellus pipistrellus*, spatial scale has to be considered for biological interpretation of light effect. At a local scale, some bats species can be concentrated in illuminated areas rather than surrounding dark places because streetlights offer new and predictable foraging opportunities by attracting a large portion of the surrounding insect biomass [25,53]. However, the impact of ALAN could be considered as negative on both nocturnal insects and bats at a larger scale because it reduces prey availability for bats in surrounding unlit landscapes by massively aggregating preys at light sources and inducing high mortality of insect (so-called “vacuum cleaner effect”, [5,25,54]). This is furthermore of particular concern as a national scale study in Great Britain showed that common species of moths have experienced rapid declines over the last 30 years [55]. This hypothesis of opposite effects of ALAN according to the spatial scale considered was confirmed by different studies (local scale: [23] vs. landscape scale: [6,56]). The studies carried out at the landscape-scale revealed negative effects of ALAN on the activity and probability of occurrence of four common species of bats: *P. pipistrellus*, *P. kuhlii*, *E. serotinus*, and *N. leisleri*, which are considered as “light attracted” species at the more local scale [22,23,24]. These hidden negative effects of ALAN at a landscape scale could also

be explained by the fact that artificial lighting does not only influence species foraging behavior, but also reproduction and commuting behaviors [57], and landscape connectivity [7].

We are currently at an important crossroad in lighting management: (i) light pollution had been increasing drastically every year for several decades in developed countries and is expanding in developing ones [2,58,59], and now (ii) lighting equipment reaches its end-of-life in developed countries. The increased cost-effectiveness of white-LEDs may contribute to an increase of ALAN through (i) the introduction of new artificial lighting sources in previously unlit areas, and (ii) the use of brighter light sources [15,16]. In this context, limiting the adverse impact of ALAN involves limiting the extent of lighting in natural habitats and sparsely urbanized habitats (removal of unnecessary light points), and maintaining areas of darkness in human-inhabited landscapes [15]. Such outdoor lighting planning requires to manage ALAN through five integrated levers of action. The two first levers raise the following questions: (i) within a landscape, which light points are necessary? (ii) during a night, what duration of lighting is necessary? Second, once areas and time periods that really need to be lit have been identified – for example for safety reasons – it should focus on (iii) the avoidance of unnecessary dispersion of light through precise directionality of the luminous flux, (iv) the drastic reduction of the proportion of UV and blue wavelengths in the spectral composition of the lamps [60], and (v) the reduction of the illuminance of light sources.

5. Conclusion

Our re-analysis clearly showed that the switches in both spectrum and intensity associated with the replacement of LPS with LED lamps strongly affected bat activity. We showed that bat activity and buzz ratio decreased with increasing LED intensity, while an opposite effect was observed with LPS lamps. Hence, the loss or the gain in bat activity when lamp types, i.e., spectrum, are switched, strongly depends on the initial and new lamp intensities. In particular, we showed that when LPS lamps are replaced by LEDs with high illuminance (i.e., >25 lux), bat activity and foraging activity are dramatically reduced. Such results stress the need to consider simultaneously the effects of changes of different light characteristics when a switch of street lighting occurs. Because switches from LPS to LED lamps can lead to an increase in light intensity, such technological change may involve a reduction of bat activity in numerous cases, especially at high LED intensities.

According to the current trend of renewal of lighting equipment, from conventional lighting technologies to LEDs that offer great opportunities to save energy and limit CO₂ emissions, we recommend to pay close attention to reduce the amount of lowest wavelengths (i.e., blue) on the LED spectrum (for example warm white LED (2500 K) instead of cool white LED (5000 K)) and reduce the lamp illuminance since both constitute main drivers of impacts on bats and their preys [30,37].

Supplementary Materials

The following are available online at <https://www.mdpi.com/1424-2818/12/4/165/s1>, Figure S1. Principal component analysis (R Pacakge *ade4*, function *dudi.pca*, Chessel D. & Dufour AB) performed on landscape variables and streetlight column characteristics among sites (Ac: control lighting column of the pair A, Ae: experimental lighting column of the pair A). The streetlight characteristics included characteristics that did not change such as the lighting height (*Height*) and characteristics that changed during the switch such as power and illuminance: *PowerBefore* is the power (Watts) in site before the switch, *PowerAfter*, power after the switch (same typology for illuminance), *ChangePower* is the difference between the power of LPS in experimental site before the switch and the power of LED after the switch (same definition for the *Changeilluminance*). Landscape variables included the distance to a wooded area (m), *Dist_Wood*, the distance to freshwater (m) *Dist_Water* and the distance to grassland (m), *Dist_Grass*. (a) eigenvalues of the PCA, Figure S2. Predicted buzz ratios of *P. pipistrellus* at control (i.e., lit using LED lamps throughout both years of the experiment) and experimental sites (i.e., lit using LED lamps only the first year and LPS lamps only the second year) before and after the switch from LPS to LED lamps under experimental sites. Results come from the BACIP modeling, Figure S3. Percentage of total explained variance, Figure S4. Relationship between bat activity (log-transformed of the number of bat passes) and illuminance (lux) at the 24 LPS streetlights in control and experimental sites before the switch, Table S1. Estimates, standard errors (SE) and *p*-value of the bat activity at control (i.e., without change of LPS lights) and experimental sites (i.e., with LPS lights switched to LED lights) before and after LPS lights were switched to LED lights. Here, the ‘reference’ category (i.e., the intercept) is ‘control’ and is identified as a category of comparison for the other categories (here ‘experimental’), Table S2. Effect of environmental variables on bat activities (β is the estimate of GLM), *p*-values were calculated using an ANOVA with a *F*-test for expressed. According to the need to adjust *p*-values for multiple comparisons, Bonferroni correction

indicates that a $\alpha = 0.05$ threshold level should be considered here as $\alpha = 0.008$, thus significant p -values in regard to Bonferroni correction are indicated in bold, * indicated that error distribution used was a quasi-Poisson instead of a negative binomial due to problem of model convergence.

Author Contributions

Conceptualization, C.K.; Formal analysis, C.K., K.B., J.P., A.R. and I.L.V.; Investigation, C.K.; Methodology, C.K., K.B. and I.L.V.; Supervision, C.K.; Validation, C.K.; Visualization, C.K., G.Z.; Writing – original draft, C.K.; Writing – review & editing, C.K., C.B., L.M., J.P., G.Z., A.R. and I.L.V. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

References

1. Falchi, F.; Cinzano, P.; Duriscoe, D.; Kyba, C.C.M.; Elvidge, C.D.; Baugh, K.; Portnov, B.A.; Rybnikova, N.A.; Furgoni, R. The new world atlas of artificial night sky brightness. *Sci. Adv.* **2016**, *2*, e1600377.
2. Hölker, F.; Moss, T.; Griefahn, B.; Kloas, W. The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy. *Ecol. Soc.* **2010**, *15*, 13.
3. Hölker, F.; Wolter, C.; Perkin, E.K.; Tockner, K. Light pollution as a biodiversity threat. *Trends Ecol. Evol.* **2010**, *25*, 681–682.
4. Navara, K.J.; Nelson, R.J. The dark side of light at night: Physiological, epidemiological, and ecological consequences. *J. Pineal R.* **2007**, *43*, 215–224.
5. Rich, C.; Longcore, T. *Ecological Consequences of Artificial Night Lighting*; Island Press: Washington, DC, USA, 2006; p. 480.

6. Azam, C.; Le Viol, I.; Julien, J.F.; Bas, Y.; Kerbiriou, C. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landsc. Ecol.* **2016**, *31*, 2471–2483.
7. Laforge, A.; Pauwels, J.; Faure, B.; Bas, Y.; Kerbiriou, C.; Fonderflick, J.; Besnard, A. Reducing light pollution improves connectivity for bats in urban landscapes. *Landsc. Ecol.* **2019**, *34*, 793–809.
8. Stone, E.L.; Jones, G.; Harris, S. Street Lighting Disturbs Commuting Bats. *Curr. Biol.* **2009**, *19*, 1123–1127.
9. Stone, E.L.; Jones, G.; Harris, S. Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Glob. Chang. Biol.* **2012**, *18*, 2458–2465.
10. Davies, T.W.; Coleman, M.; Griffith, K.M.; Jenkins, S.R. Night-time lighting alters the composition of marine epifaunal communities. *Biol. Lett.* **2015**, *11*, 20150080.
11. Minnaar, C.; Boyles, J.G.; Minnaar, I.A.; Sole, C.L.; Mckechnie, A.E. Stacking the odds: Light pollution may shift the balance in an ancient predator–prey arms race. *J. Appl. Ecol.* **2015**, *52*, 522–531.
12. Bennie, J.; Davies, T.W.; Cruse, D.; Inger, R.; Gaston, K.J. Cascading effects of artificial light at night: Resource-mediated control of herbivores in a grassland ecosystem. *Philos. Trans. R. Soc. B* **2015**, *370*, 20140131.
13. European Commission. The European GreenLight Programme Efficient Lighting Project Implementation Catalogue 2005–2009. 2011. Available online: https://publications.jrc.ec.europa.eu/repository/bitstream/JRC62317/reqno_jrc62317_lb-na-24689-en.pdf (accessed on 27 March 2020).
14. Almeida, P.S.; Braga, H.A.C.; Dalla Costa, M.A.; Alonso, J.M. Offline Soft-Switched LED Driver Based on an Integrated Bridgeless Boost–Asymmetrical Half-Bridge Converter. *IEEE Trans. Ind. Appl.* **2015**, *51*, 761–769.
15. Kyba, C.C.M.; Hänel, A.; Höcker, F. Redefining efficiency for outdoor lighting. *Energy Environ. Sci.* **2014**, *7*, 1806–1809.
16. Update on the Status of LED Market. Publications Office of the European Union, 2014. Available online: <https://publications.jrc.ec.europa.eu/repository/bitstream/JRC92971/jrc92971%20online.pdf> (accessed on 27 March 2020).
17. Rowse, E.G.; Harris, S.; Jones, G. The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights. *PLoS ONE* **2016**, *11*, e0150884.

18. Aubé, M.; Roby, J.; Kocifaj, M. Evaluating Potential Spectral Impacts of Various Artificial Lights on Melatonin Suppression, Photosynthesis, and StarVisibility. *PLoS ONE* **2013**, *8*, e67798.
19. Dominoni, D.M.; Quetting, M.; Partecke, J. Long-Term Effects of Chronic Light Pollution on Seasonal Functions of European Blackbirds (*Turdus merula*). *PLoS ONE* **2013**, *8*, e85069.
20. Durrant, J.; Michaelides, E.B.; Rupasinghe, T.; Tull, D.; Green, M.P.; Jones, T.M. Constant illumination reduces circulating melatonin and impairs immune function in the cricket *Teleogryllus commodus*. *PeerJ* **2015**, *3*, e1075.
21. van Langevelde, F.; Ettema, J.A.; Donners, M.; WallisDeVries, M.F.; Groenendijk, D. Effect of spectral composition of artificial light on the attraction of moths. *Biol. Conserv.* **2011**, *144*, 2274–2281.
22. Rydell, J. Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* **1992**, *6*, 744–750.
23. Azam, C.; Kerbiriou, C.; Vernet, A.; Julien, J.F.; Bas, Y.; Plichard, L.; Maratrat, J.; Le Viol, I. Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats? *Glob. Chang. Biol.* **2015**, *21*, 4333–4341.
24. Lacoëuilhe, A.; Machon, N.; Julien, J.-F.; Le Bocq, A.; Kerbiriou, C. The influence of low intensities of light pollution on bat communities in a semi-natural context. *PLoS ONE* **2014**, *9*, e103042.
25. Eisenbeis, G. Artificial night lighting and insects: Attraction of insects to streetlamps in a rural setting in Germany. In *Ecological Consequences of Artificial Night Lighting*; Rich, C., Longcore, T., Eds.; Island Press: Washington, DC, USA, 2006; pp. 281–304.
26. Rydell, J. Bats and Their Insect Prey at Streetlights. In *Ecological Consequences of Artificial Night Lighting*; Rich, C., Longcore, T., Eds.; Island Press: Washington, DC, USA, 2006; pp. 43–60.
27. Stone, E.; Zeale, M.R.K.; Newson, S.E.; Browne, W.J.; Harris, S.; Jones, G. Managing Conflict between Bats and Humans: The Response of Soprano Pipistrelles (*Pipistrellus pygmaeus*) to Exclusion from Roosts in Houses. *PLoS ONE* **2015**, *10*, e0131825.
28. Azam, C.; Le Viol, I.; Bas, Y.; Zissis, G.; Vernet, A.; Julien, J.F.; Kerbiriou, C. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landsc. Urban Plan.* **2018**, *175*, 123–135.
29. Zuur, A.; Ieno, E.N.; Walker, N.; Saveliev, A.A.; Smith, G.M. *Mixed Effects Models and Extensions in Ecology with R*; Springer: New York, NY, USA, 2009; pp. 322–342.

30. Owens, A.C.S.; Lewis, S.M. The impact of artificial light at night on nocturnal insects: A review and synthesis. *Ecol. Evol.* **2018**, 11337–11358.
31. Jones, G.; Rydell, J. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philos. Trans. R. Soc. B.* **1994**, 346, 445–455.
32. Rydell, J.; Entwistle, A.; Racey, A. Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk. *Oikos* **1996**, 76, 243–252.
33. Mickleburgh, S.P.; Hutson, A.M.; Racey, P.A. A review of the global conservation status of bats. *Oryx* **2002**, 36, 18–34.
34. Arlettaz, R.; Godat, S.; Meyer, H. Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biol. Conserv.* **2000**, 93, 55–60.
35. Robinson, M.F.; Stebbings, R.E. Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *J. Zool.* **1997**, 243, 117–136.
36. Safi, K.; König, B.; Kerth, G. Sex differences in population genetics, home range size and habitat use of the parti-colored bat (*Vespertilio murinus*, Linnaeus 1758) in Switzerland and their consequences for conservation. *Biol. Conserv.* **2007**, 137, 28–36.
37. Spoelstra, K.; van Grunsven, R.H.A.; Ramakers, J.J.C.; Ferguson, K.B.; Raap, T.; Donners, M.; Veenendaal, E.M.; Visser, M.E. 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. Ser. B-Biol. Soc.* **2017**, 284, 1855.
38. Obrist, M.K.; Boesch, R.; Flückiger, P.F. Variability in echolocation call design of 26 Swiss bat species: Consequences, limits and options for automated field identification with a synergetic pattern recognition approach. *Mammalia* **2004**, 68, 307–322.
39. Britton, A.R.; Jones, G. Echolocation behaviour and prey-capture success in foraging bats: Laboratory and field experiments on *Myotis daubentonii*. *J. Exp. Biol.* **1999**, 202, 1793–1801.
40. Hayes, J.P. Temporal Variation in Activity of Bats and the Design of Echolocation-Monitoring Studies. *J. Mam.* **1997**, 78, 21.
41. O'Donnell, C.F.J. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *N. Z. J. Zool.* **2000**, 27, 207–221.
42. Ciechanowski, M.; Zajac, T.; Bilas, A.; Dunajski, R. Spatiotemporal variation in activity of bat species differing in hunting tactics: Effects of weather, moonlight, food abundance, and structural clutter. *Can. J. Zool.* **2007**, 85, 1249–1263.

43. Newson, S.E.; Evans, H.E.; Gillings, S. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biol. Conserv.* **2015**, *191*, 38–49.
44. Generalized Linear Mixed Models Using Template Model Builder. 2020. Available online: <http://cran.uni-muenster.de/web/packages/glmmTMB/glmmTMB.pdf> (accessed on 27 March 2020).
45. Freckleton, R.P. On the misuse of residuals in ecology: Regression of residuals vs. multiple regression. *J. Anim. Ecol.* **2002**, *71*, 542–545.
46. Kerbiriou, C.; Bas, Y.; Le Viol, I.; Lorrillière, R.; Mougnot, J.; Julien, J.F. Bat Pass Duration Measurement: An Indirect Measure of Distance of Detection. *Diversity* **2019**, *11*, 47.
47. Zuur, A.; Ieno, E.N.; Elphick, C.S. A protocol for data exploration to avoid common statistical problems. *Meth. Ecol. Evol.* **2010**, *1*, 3–14.
48. Dominoni, D.M.; Nelson, R.J. Artificial light at night as an environmental pollutant: An integrative approach across taxa, biological functions, and scientific disciplines. *J. Exp. Zool.* **2018**, *329*, 387–393.
49. Polak, T.; Korine, C.; Yair, S.; Holderied, M.W. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. *J. Zool.* **2011**, *285*, 21–27.
50. Boldogh, S.; Dobrosi, D.; Samu, P. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterol.* **2007**, *9*, 527–534.
51. Stone, E.L.; Wakefield, A.; Harris, S.; Jones, G. The impacts of new street light technologies: Experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide. *Philos. Trans. R. Soc. B* **2015**, *370*, 20140127.
52. Lewanzik, D.; Voigt, C.C. Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *J. Appl. Ecol.* **2017**, *54*, 264–271.
53. Perkin, E.K.; Hölker, F.; Tockner, K.; Richardson, J.S. Artificial light as a disturbance to light-naïve streams. *Freshw. Biol.* **2014**, *59*, 2235–2244.
54. Grubisic, M.; van Grunsven, R.; Kyba, C.; Manfrin, A.; Hölker, F. Insect declines and agroecosystems: Does light pollution matter? *Ann. Appl. Biol.* **2018**, *173*, 180–189.
55. Conrad, K.F.; Warren, M.S.; Fox, R.; Parsons, M.S.; Woiwod, I.P. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* **2006**, *132*, 279–291.

56. Pauwels, J.; Le Viol, I.; Azam, C.; Valet, N.; Julien, J.F.; Bas, Y.; Lemarchand, C.; de Miguel, A.S.; Kerbiriou, C. Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landscape Urban Plan.* **2019**, *183*, 12–25.
57. Hale, J.D.; Fairbrass, A.J.; Matthews, T.J.; Davies, G.; Sadler, J.P. The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats. *Glob. Chang. Biol.* **2015**, *21*, 2467–2478.
58. Bennie, J.; Davies, T.W.; Inger, R.; Gaston, K.J. Mapping artificial lightscapes for ecological studies. *Met. Ecol. Evol.* **2014**, *5*, 534–540.
59. Sánchez de Miguel, A.; Aubé, M.; Zamorano, J.; Kocifaj, M.; Roby, J.; Tapia, C. Sky Quality Meter measurements in a colour-changing world. *Mon. Not. R. Astron. Soc.* **2017**, *467*, 2966–2979.
60. Gaston, K.J.; Davies, T.W.; Bennie, J.; Hopkins, J. REVIEW: Reducing the ecological consequences of night-time light pollution: Options and developments. *J. Appl. Ecol.* **2012**, *49*, 1256–1266.

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Supplementary material (*available in the Appendix IV at the end of this PhD*)

Supplementary Material 1: Radiometric and Photometric Quantities

Supplementary Material 2: Composition of landscape variables and streetlight column characteristics among sites.

Supplementary Material 3: Comparison of the results of parametric and non-parametric approaches when changes in light intensity are not taken into account

Supplementary Material 4: assessment of the relative importance of environmental variables on bat activity before the experiment of shift from LPS to LED, thus only under LPS streetlight

In short

RESULTS



Kerbiriou et al. (2020)

Figure 29: Results of Kerbiriou et al. (2020)

Main novelties:

- Effect of switching from sodium vapor lamps (here LPS lamps) to LEDs on bat activity.
- Existence of an interaction between the emission spectrum and light intensity on bat activity (i.e. the effect of light intensity on bats varies according to the emission spectrum of the lamp).

Results (Figure 29):

We showed that when switching from LPS lamps to LEDs, the change in the emission spectrum and light intensity (characterised either by illuminance or power) has significant interactive effects on four of the five bat activity metrics studied (total bat activity, *P. pipistrellus* activity, *Nyctalus* spp. activity and *P. pipistrellus* feeding buzz ratio). Thus, the positive or negative effect of the change in spectrum depends strongly on the intensity of the old and new lamps. As expected, at low intensities, bat activity was higher around the LEDs than around the LPS lamps, while, at high intensities, it was the opposite. In other words, bat activity decreased with increasing light intensity around LEDs, while it increased with increasing light intensity around LPS lamps. Such results raise the need to consider not only the change in spectrum when retrofitting old lighting technologies, but also in light intensity, as, in many cases, the switch might result in a reduction of bat activity, especially when the intensity of the new LEDs is high.

Perspectives

In this study, we showed that when investigating the effects of the replacement of lighting technologies on biodiversity, not only changes in the emission spectrum should be taken into account, but also changes in other lighting parameters, such as illuminance or directivity of the luminous flux, and the possible interactions between these parameters.

It has been predicted that by 2027, 89 % of the world's streetlights will use LEDs (estimated over 125 countries by the Northeast Group, Zissis et al., 2021). Such a prediction may seem to be dramatic as we showed, in this chapter, that this could have important consequences for biodiversity despite its non-neglectable potential to reduce the carbon footprint of lighting. Indeed, this replacement of conventional lighting equipment with LEDs may be accompanied by an increase in light intensity and, as “broad white” LEDs are currently the most widely used, it will likely lead to a “whitening” of ALAN.

However, as the LED technology is highly flexible, it is possible to select the minimum required light intensity, and to adapt the light spectra to reduce emissions at wavelengths that alter biological processes and disrupt organisms (Sánchez de Miguel et al., 2022). Some studies have already investigated whether LEDs have a different effect on bats depending on their colour. Although some of them did not find different effects of LEDs depending on the colour in some contexts (Bolliger et al., 2020; Spoelstra et al., 2018), others tend to show that red or amber lights might be less disturbing to bats than white or green ones (Barré et al., 2021a; Spoelstra et al., 2017; Straka et al., 2020). More generally, these less harmful effects of amber and red LEDs on biodiversity have been found for other taxa (e.g. birds: Aulsebrook et al., 2020; Kernbach et al., 2020, insects: Davies et al., 2017; Owens et al., 2018). Thus, even if some counterexamples have been documented (e.g. Briolat et al., 2021), amber and red LEDs have been advocated in recent years, as they seem generally to be less damaging to biodiversity than white ones.

Furthermore, it should be reminded that the colour of a light source can be defined by the emission spectrum (i.e. the distribution of the wavelengths emitted) or by the CCT (the colour appearance of the light emitted by a light source) (see **Box 1**). These two measures are not equivalent, for instance, several lights that could be defined as “amber” according to their CCT can have a broader or narrower emission spectrum (e.g. the spectrum of the amber LED used in Briolat et al., (2021) is broader than that used in Straka et al. (2020) and both are wider than the spectrum of a conventional LPS lamp). Thus, besides preferring red and amber LEDs to those emitting shorter wavelengths, it would likely be less damaging to biodiversity to

choose the narrowest possible emission spectrum (i.e. the least likely to trigger a biological response).

As shown in the precedent chapters of this PhD, when studying the impact of light pollution, researchers should consider multiple temporal and spatial scales. A study such as the one presented in this chapter, allows to show that light characteristics modulate bats' responses to ALAN and disrupt their behaviours. However, such a study does not allow to conclude whether local attraction is, for instance, beneficial for “light tolerant” bat species, hence the need to also focus on wider temporal and spatial scales which better reflect long-term effect of ALAN on populations.

Studying the effect of ALAN on biodiversity at the landscape scale requires to have access to light data covering the whole study area. Most studies conducted at this scale used the radiance data (in $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$) from the average radiance composite raster produced by the Earth Observation Group using night-time data from the Visible Infrared Imaging Radiometer Suite (VIIRS) Day/Night Band (Elvidge et al., 2021) (e.g. Azam et al., 2016; Barré et al., 2021b; Froidevaux et al., 2017; Korpach et al., 2022; Laforge et al., 2019; Lewanzik et al., 2021; Mariton et al., 2022; Miller et al., 2017; Rodríguez et al., 2015). These radiance measurements are made in a spectral band of 500 to 900 nm (Kyba et al., 2017a).

However, the current switch to LEDs results in increased emissions in visible wavelengths, especially in the blue part of the spectrum, which is not detected by the satellite sensors used to produce the VIIRS dataset (Sánchez de Miguel et al., 2022). Then, a switch from old lighting technologies, such as LPS or HPS lamps, to LEDs might lead to a decrease in the radiance measured by the sensors (Kyba et al., 2017a). Thus, to study the effect of the development of LEDs at the landscape scale, other sources of data should be used.

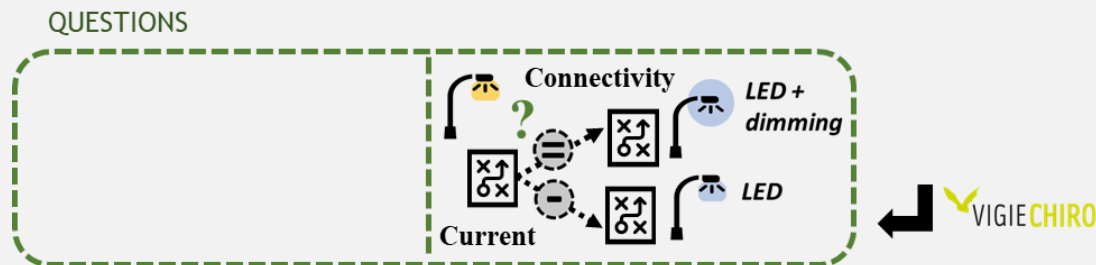
Sánchez de Miguel et al. (2021) advocated the use of the night-time images taken with the Digital single-lens reflex camera (DSLR) from the International Space Station (ISS) as they are the only current visible multispectral data available to date. After substantial processing and calibration of these images, the intensities and ratios of the RGB channels can be exploited. In particular, these data have already been used in Pauwels et al. (2019). They showed that the ISS pictures were the best predictors of the negative effect of ALAN on *P. pipistrellus* activity at the city scale compared to the VIIRS dataset and ground data (i.e. location of streetlights).

These multispectral pictures could therefore offer the possibility of assessing – or at least predicting (see **Box 7**) – the impact of switching from conventional lighting technologies to LEDs at wide scales, which is an urgent need, especially for designing biodiversity-friendly lighting schemes.



Box 7: Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas (in prep)

Pauwels J., Le Viol I., Mariton L., Laforge A., Bas Y., Coulon A., Valet N., Besnard A., Fonderflick J., Kerbiriou C., (in prep)



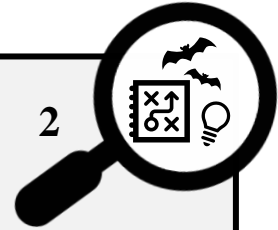
Pauwels et al. (in prep)

Questions of Pauwels et al (in prep)

Context:

In many developing regions, lighting equipment is reaching the end of its life and conventional lighting technologies (e.g. LPS, HPS, HPM, MH), which are considered to be energy-consuming, are gradually being replaced by LEDs with much higher luminous efficiency (Gaston and de Miguel, 2022; Kyba, 2018). Most LEDs currently in use have a broader spectrum and are richer in blue light (Kyba, 2018) compared to sodium vapour lamps (**Figure 3**). Some authors warn of a potential “rebound effect”, as the increasing cost-effectiveness of LEDs could lead to an increase number of light sources and/or an increase in light intensity (Gaston and de Miguel, 2022; Höölker et al., 2010; Kyba, 2018). Conversely, LEDs have more directional flux and are generally implemented in fixtures that better concentrate light towards the area to be illuminated, thus limiting light trespass into areas that are not intended to be lit.

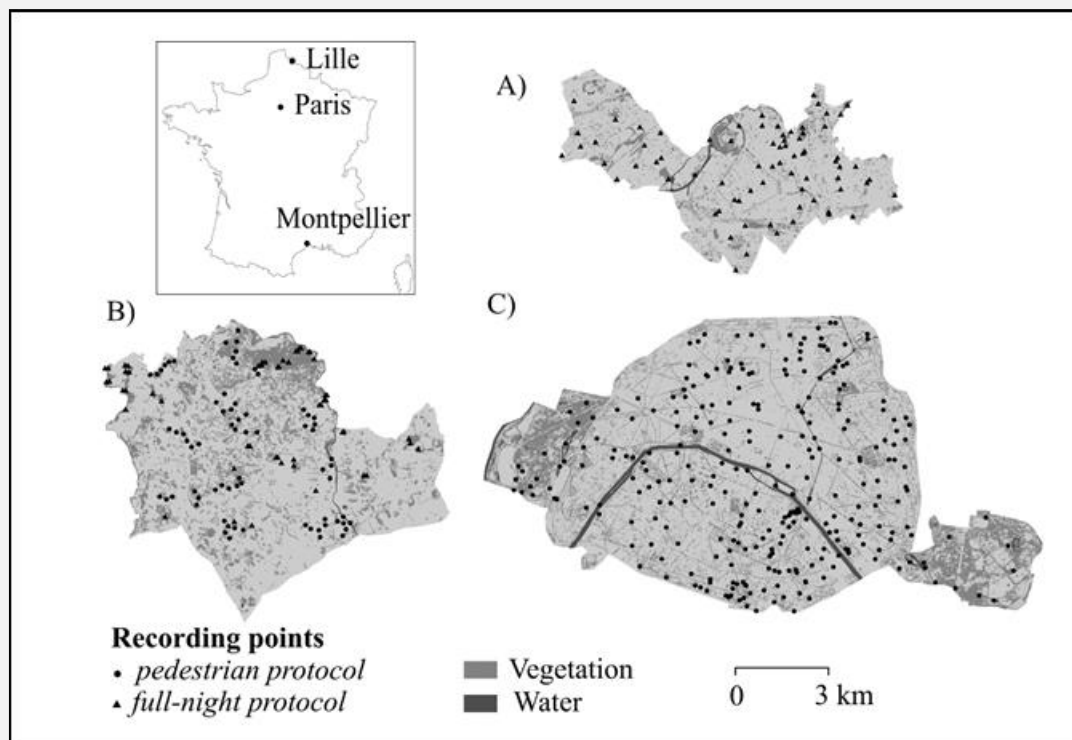
It is crucial to assess how this predicted large and rapid deployment of LEDs in public outdoor lighting impacts biodiversity. In particular, the broader emission spectrum of LEDs, with more blue wavelengths than conventional sodium lamps, raises concerns because of the wide range of processes or organisms it might disrupt (Gaston and de Miguel, 2022). However, very few studies have assessed the impacts of this change in lighting technology on biodiversity, almost all have been conducted at local scales and none considered possible changes in functional connectivity. Yet, being able to move across the landscape is essential to fulfil daily requirements (e.g. food, shelter) and to maintain population viability (Fischer and Lindenmayer, 2007). Laforge et al. (2019) showed that ALAN could disrupt the ability of bats to move across urban areas where landscapes are already highly fragmented, even for



Box 7: Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas

“light tolerant” species, with potential cascading effects on population dynamics. Thus, it is of utmost interest to assess whether the adoption of LEDs could lead to an even lower connectivity at city scale.

We investigated how changes in ALAN attributes (i.e. spectrum, radiance) due to the expected transition to LEDs will impact functional connectivity for bats in three major French cities (Paris, Lille, Montpellier). Our objectives were (i) to measure the current effect of ALAN on landscape connectivity for bats, (ii) to evaluate how the expected transition to LEDs will affect light pollution (i.e. spectrum, radiance) and landscape connectivity (iii) to determine



Study sites: Lille (A), Montpellier (B), and Paris (C). Light levels are 20 to 40 times higher than natural light levels in Lille and Montpellier and over 40 times higher in Paris (Falchi et al., 2016). Light levels are 20 to 40 times higher than natural light levels in Lille and Montpellier and over 40 times higher in Paris (Falchi et al., 2016). The Blue/Green ratio in the original ISS picture was 0.38 in Paris, 0.36 in Lille and 0.30 in Montpellier. Tree cover represents 21% of the surface in Paris and Montpellier and 14% of the surface in Lille. Paris, the largest of the three cities (105 km²), has 17 parks (mean size 0.13 km²) in its center and two woodlands on its borders (10 and 8.5 km²); Lille (35 km²) has a dozen parks (mean size 0.15 km²); and Montpellier (57 km²) has a large number of parks of various sizes spread across the city, the largest one being 1 km².



Box 7: Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas

whether this evolution of lighting technology will have different effects depending on the city considered (i.e. landscape context). We predicted that, due to LED important proportion of blue wavelengths, the change in lighting technology will have a negative impact on landscape connectivity for bats but that a better orientation of the light flux may help reduce this impact.

Abstract of the material and methods:

We used fine scale night-time pictures taken from the International Space Station (ISS), which became more accessible through the citizen science program Cities at Night (<http://citiesatnight.org/>) (Sánchez de Miguel et al., 2021). As they were composed of four colour bands (one blue, one red and two green), we had information on the spectral distribution of the emissions and we were able to simulate different outdoor lightning scenarios at the city scale.

We assessed and compared landscape connectivity for bats under four situations: 1) current state of lighting; 2) ‘No Light scenario’; 3) ‘LED scenario’ reflecting the shift of lighting technology towards 3000 K LEDs, with the number of light sources and radiance level remaining unchanged; and 4) ‘LED30 scenario’, similar to the LED scenario but with a 30 % decrease in pixel radiance to simulate the more directional flux of LEDs that may reduce overall light emissions (Aubé et al., 2018). Our workflow was the following one:

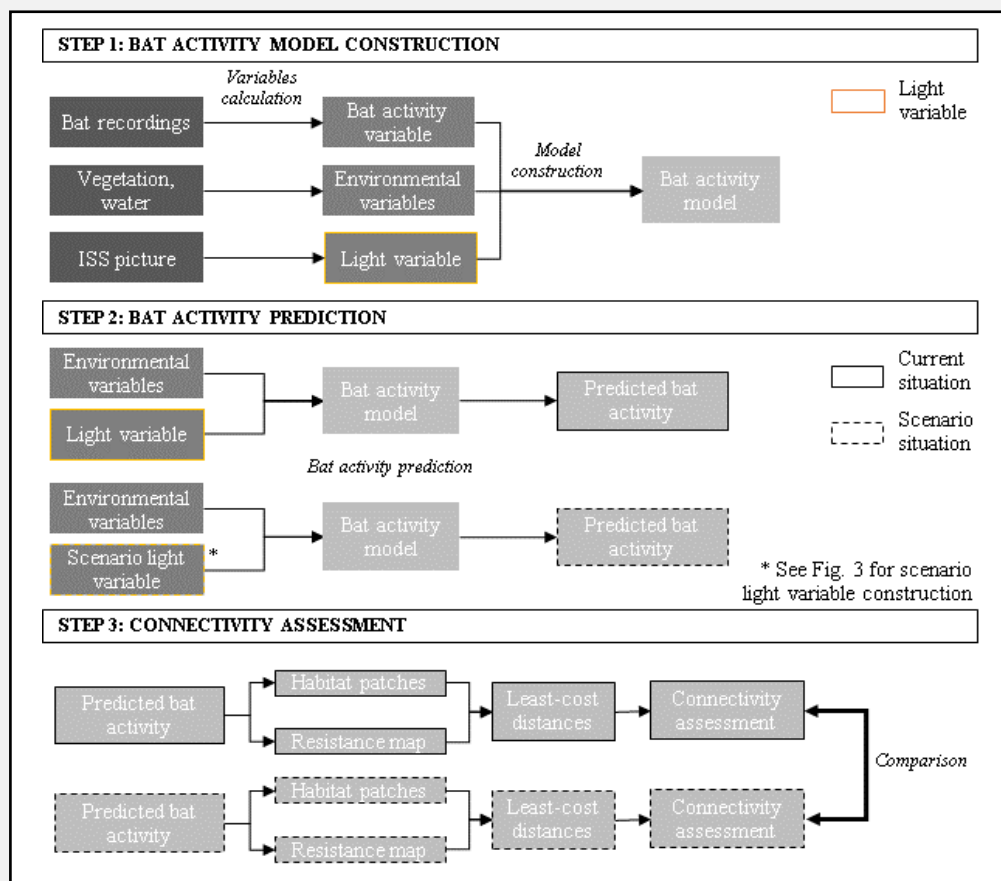
(1) We used data from the citizen science program Vigie-Chiro and data provided by the project “TRAME NOIRE” (Lille, Laforge et al., 2019). We only had sufficient data to perform the analysis in the three cities for *P. pipistrellus*, which is a “light tolerant” species often found in urban areas (Russo and Ancillotto, 2015) and one of the most common species in France although its populations tend to decline (Bas et al., 2020). Bat activity was recorded using the setting of the Vigie-Chiro program between June and October 2008 to 2015. *P. pipistrellus* passes recorded during the two first hours after sunset were used (282, 153 and 73 sites monitored for Paris, Montpellier and Lille respectively). Our connectivity modelling approach was based on the hypothesis that bat activity is a proxy of habitat suitability in terms of food resources and accessibility (Frey-Ehrenbold et al., 2013; Mimet et al., 2020; Pinaud et al., 2018) and could be used to derive a resistance surface.



Box 7: Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas

(2) Using generalized linear mixed models (GLMMs), we estimated the relationship between bat activity and environmental covariates, including ALAN. Using the predictions from these GLMMs, we derived a resistance surface (Cushman et al., 2014). We then used the least-cost path (LCP) method to identify highly connected areas (Balbi et al., 2019) within each city.

(3) We simulated the three lighting modification scenarios and assessed how these alterations affect landscape connectivity compared to the current situation.



Workflow followed

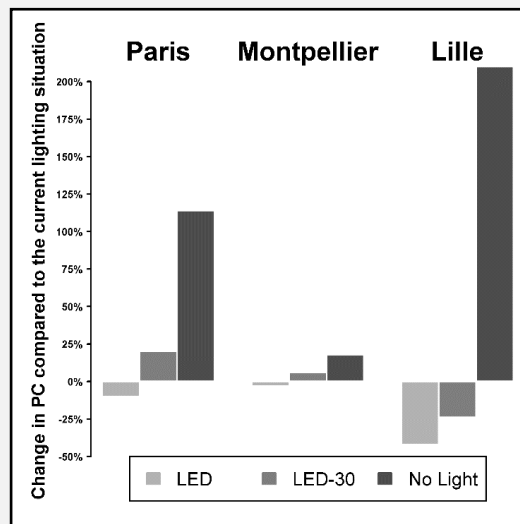
Results and discussion:

We confirmed that light had a significant negative effect on both activity and landscape functional connectivity for *P. pipistrellus*. We validated our prediction that a switch to LEDs would further decrease landscape connectivity for bats by increasing radiance and light emissions at short wavelengths compared to the current, already heavily light-polluted situation. Yet, a reduced light intensity or a better orientation of the light flux as the one



Box 7: Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas

simulated through the “LED-30 scenario” may help to reduce the negative impact of light pollution; however, it would depend on the context of a given city (i.e. on the landscape composition).



Change in overall landscape connectivity for the lighting scenarios compared to the current situation.

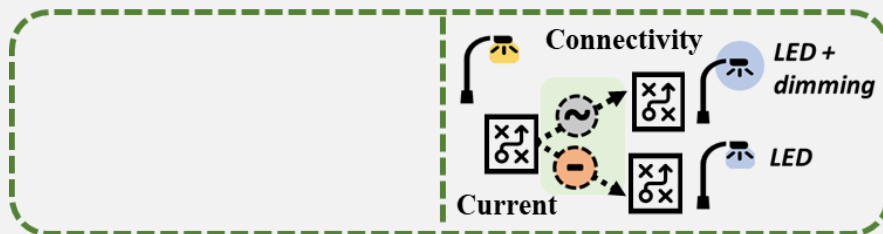
The degree of impact of our outdoor lighting scenarios, simulating technological evolution, on landscape connectivity for bats varied considerably between cities. The negative effect of the “LED scenario” on landscape connectivity for *P. pipistrellus* was highest in Lille and lowest in Montpellier. The variation in overall connectivity across all scenarios was weak for Montpellier which may be due to the fact that initially 42% of the extended area was unlit (compared to 29% for Lille and 15% for Paris). It suggests that the switch from pressure sodium lamps to LEDs may have a weak influence on bats in urban areas with large proportions of unlit areas. Paris had an initial radiance with a Blue/Green ratio of 0.38 in the original ISS picture compared to 0.36 for Lille, which is closer to the ratio of 0.4 applied to mimic the spectrum of 3000K LEDs in this study. The transition to LEDs may thus have a greater negative impact on connectivity for bats in Lille than in Paris, because it involves greater changes in radiance compared to their respective initial situations. Our results therefore show that it is not straightforward to estimate the influence of a change in lighting technology, as it depends on many factors such as the initial level and characteristics of light pollution, the size and distribution of suitable habitat patches in the landscape and probably even more (e.g. the spatial distribution of light sources or the life-history traits of species).



Box 7 : Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas

It should not be forgotten that *P. pipistrellus* is a species usually considered to be “light tolerant”, so more light sensitive bat species may suffer even greater impacts. This highlights the importance to account for biodiversity in lighting planning to help species maintain or recolonise cities (Laforge et al., 2019; Pauwels et al., 2019). Removing light points and avoiding lighting new areas are still likely the most effective measures to restore and not to alter functional connectivity for bats. Where lights have to be used, LEDs with warmer colours (i.e. amber or red light) should be preferred to protect bats from light pollution.

RESULTS



Pauwels et al. (in prep)

Results of Pauwels et al. (in prep)



General discussion

“And when a flock of bluebills, pitching pondward, tears the dark silk of heaven in one long rending nose-dive, you catch your breath at the sound, but there is nothing to see except stars.”

Aldo Leopold, A Sand County Almanac

1. Principal results

(Figure 30)

The main novelty of this research on the impacts of ALAN on biodiversity is to assess the potential effectiveness of various mitigation measures at multiple spatial scales (local: **Kerbiriou et al. (2020)**, city scale: **Pauwels et al., (in prep) (Box 7)**, national scale: **Mariton et al., 2022, (accepted)** and **Box 6**) but also temporal scales (**Mariton et al., 2022, (accepted)** and **Box 6**).

To our knowledge, to date, conservation measures aimed at mitigating the impacts of anthropogenic pressures on biodiversity often fail to take into account the temporal niche of species, which is sometimes poorly known. The development of citizen science programs coupled with PAM allows the collection of large-scale data that could provide new information on the ecology of species. Using such data, we characterised the diel activity patterns of 20 bat species and illustrated how this knowledge of the temporal ecology of target species, in this case bats, could contribute to the improvement of existing mitigation measures and help create new ones (**Mariton et al., (accepted)**).

In particular, a major lever put forward in the literature to mitigate the negative impacts of light pollution on biodiversity is to limit the duration of lighting. However, current PNL schemes do not cover the activity peaks of most bat species and are therefore unable to fully reduce the impacts of ALAN on bats (Azam et al., 2015; Day et al., 2015; Hooker et al., 2022). In order to cover, at least, the activity of the latest-emerging bat species, which are among the most light-sensitive species, they should start much earlier. However, such an earlier switch-off time would probably be difficult to implement because it also corresponds to the times when humans most need light for their activities. Switching off lights during the peak periods

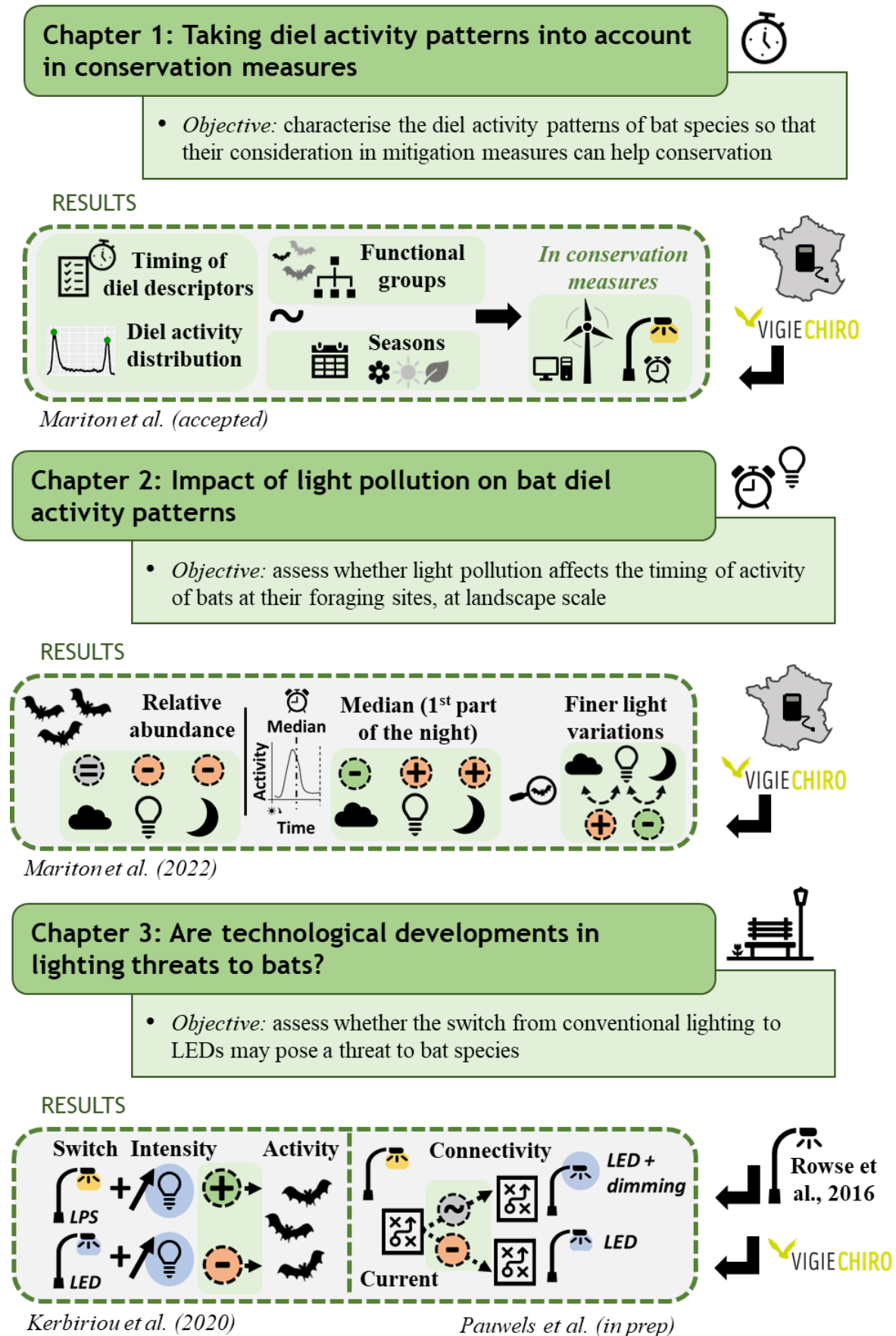


Figure 30: Principal results of this PhD

of other species' activities might even be equivalent to not switching on lights between sunset and sunrise.

We therefore wondered about the sensitivity of the species that emerge earliest at night and that are for the most part considered to be “light tolerant”. The responses of these species to light pollution vary according to the spatial scale considered, they seem to be favoured locally by the presence of ALAN but to be less abundant because of it at the landscape scale (Azam et al., 2016). We showed that considering the temporal scale could provide an explanation for these contrasted responses. We found that the activity of a “light tolerant” species (*E. serotinus*, open-space-foraging species) decreased in illuminated landscapes (Mariton et al., 2022). *E. serotinus* activity was also delayed because of ALAN, and this delay was greater on overcast nights, probably because cloud cover increased skyglow in light-polluted areas. By reducing the time-budget of bats to forage and/or by causing a desynchronisation with the activity peak of their prey, this delay could have important consequences for individual fitness and population dynamics, which could explain the lower abundance of this species at the landscape scale. The preliminary results presented in **Box 6** indicate that at least four other species belonging to the edge- and open-space-foraging guilds (which are considered to be “light tolerant” guilds) may show lower abundance and/or delayed activity in light-polluted landscapes. These species may thus be wrongly described as “light tolerant” and it seems essential to also protect them from light pollution.

Where and when it is not possible to switch off the lights, technical parameters can be modified to reduce the impact of ALAN on biodiversity. Currently, in many countries, lighting equipment is reaching the end of its life and is being replaced by LEDs. Although this technology allows energy savings, it is a cause of concern for ecologists. Indeed, the most commonly used LEDs have a broad emission spectrum that can impact many biological processes and taxa (Sánchez de Miguel et al., 2022). In addition, the higher luminous efficacy of LEDs raises concerns about a “rebound effect” (Kyba et al., 2017a) leading to increased use of lighting both in terms of spatial extent and intensity. However, the effect of these equipment changes has been little studied to date and simultaneous consideration of changes in different lighting parameters is sometimes lacking.

We showed that switching from LPS lamps to LEDs with an increase in intensity had additive and interactive negative effects on bat activity (Kerbiriou et al., 2020). At the landscape scale, we showed that the adoption of LEDs would drastically reduce landscape connectivity for a “light tolerant” species, presaging even greater impacts for other species (Pauwels et al., *in prep*) (**Box 7**). However, better directionality (and thus lower radiance of

ALAN at city scale) of the new lighting could help mitigate for this effect by reducing the amount of light contributing to the skyglow. Therefore, where light cannot be switched off, we recommended using LEDs with warmer colours (e.g. “amber” or “red” LEDs), reduced intensity and better directionality.

2. A prerequisite for designing and promoting mitigation measures: understanding and assessing the impact of ALAN on biodiversity

Understanding the mechanisms by which ALAN disrupts ecological processes and organisms is an essential prerequisite for combating light pollution. This knowledge can then be used as a basis for promoting action and constructing effective conservation measures. The multiscale and multidimensional studies presented in this PhD add to a growing body of literature on the impact of ALAN on bats. As a conservation biologist we can now ask ourselves to what extent this rich scientific literature might allow us to answer (or infer an answer to) the following question: can the new biotic and abiotic conditions resulting from the intrusion of ALAN threaten the persistence bat populations? Indeed, such knowledge could make it possible to better assess the importance of the contribution of light pollution to the decline of certain bat populations and could support the urgent need to implement multi-scale conservation measures.

2.1 Alteration of abiotic conditions by ALAN

Firstly, it should be remembered that light is a major abiotic cue for biodiversity. The alteration of the natural light levels and light-dark cycles could therefore directly affect bat species through different mechanisms. In **Mariton et al., (2022)** and in the **Box 6**, we found that some bat species tended to delay their activity in light-polluted landscapes. One explanation to this result is that ALAN, as an abiotic cue, could directly alter biological timings. Indeed, at the day scale, natural light has been shown to be a major parameter entertaining circadian rhythms (Aschoff, 1989; Erkert, 1982). To date, no studies have investigated the effect of ALAN on the circadian rhythm of bats. However, ALAN could result in alterations in these rhythms and thus have cascading consequences on the physiology and behaviours of bats. Furthermore, as it has been shown for other species (e.g. de Jong et al., 2015; Le Tallec et al., 2015; Senzaki et al., 2020), light pollution could alter bat phenology by masking natural

variations in night lengths. However, to our knowledge, to date, almost no study has investigated this potential effect of ALAN.

In **Kerbiriou et al. (2020)**, we found that bat activity decreased with increasing LED intensity while an opposite effect was observed with LPS lamps. We hypothesised that this difference in response could be explained by the fact that LED light was closer to daylight than LPS light, making bats fear greater risks of predation. However, this also raises the question of bats' vision and, in particular, how they perceive colours and whether they could be blinded or disoriented by lights (however, see Orbach and Fenton, 2010), especially if the intensity is high and/or the emission spectrum is similar to that of daylight. However, to date, we lack studies on bats' vision and their perception of colours (however, see for instance Müller et al., 2009). A better knowledge of bats' vision could also make it possible to better evaluate whether the photometric measurements (e.g. illuminance in lux) commonly measured in the field can really constitute a good proxy for the intensity of the light perceived by bats (see questions raised **Box 5**).

2.2 Alteration of biotic conditions by ALAN

In the literature, alterations of biotic conditions are most often put forward to explain the observed responses of bats to light pollution. In particular, the most widely accepted hypothesis is that bats' reactions to ALAN would be driven by a trade-off between the availability of prey and the risk of predation (actual or perceived). As a matter of fact, as insects are attracted by light sources, bats might be willing to forage near ALAN to exploit this predictable insect biomass (Stone et al., 2015a) and perhaps to cope with a reduction in food resources in dark areas near lit ones (this depletion of insects from dark areas has been termed a “vacuum cleaner” effect (Eisenbeis, 2006)). However, ALAN could also increase the actual – or at least perceived – risk of predation for bats by increasing the efficiency of predators using vision and by allowing diurnal predators to be active later in the night (Jones and Rydell, 1994; Rydell et al., 1996). Therefore, bats would only take risks by being active under higher light levels if the nutrient gains outweigh the risk of predation. This hypothesis has gained credibility through its explanatory power for the results of studies such as those presented in this PhD. It would explain why the responses of bats to light pollution depend on:

- (1) *The species under consideration*: at the local scale, edge- and open-space-foraging species would be attracted by light sources and the insects clustered at their vicinity because their fast and agile flight would lead to less risks of predation in contrast to

narrow-space-foraging species, which have a low and slow flight (Rydell, 1992)). Similarly, this would explain why most open- and edge-space-foraging species are active earlier in the night (when the activity of the insects they feed on is highest) than narrow-space-foraging species (**Mariton et al., (accepted)**), which would only start to be active when the risk of predation is lower.

- (2) *The behaviour under consideration*: while edge- and open-space-foraging species are attracted to light locally when foraging, they avoid ALAN when commuting. This could be explained by the fact that when they forage, they are willing to take risks to exploit the insect biomass near light sources, whereas when they commute, they prefer dark areas to avoid predation (explaining lower functional connectivity for bats in light-polluted landscapes as shown in **Hale et al., 2015; Laforge et al., 2019; Pauwels et al., (in prep)**).
- (3) *The time of the year*: bat would be more willing to take risks when their energy requirements are higher, which would explain, for instance, the delayed activity of some bat species due to ALAN during gestation but not during lactation (**Box 6**).
- (4) *The light characteristics*: the perception of increased predation would be likely to be stronger, for instance, when light levels are higher and when the light spectrum is closer to daylight (**Kerbiriou et al., 2020**).

However, although it has long been shown that “light tolerant” bat species do forage under streetlights (Rydell, 1992), the link between higher light levels and actual or perceived increased risk of predation has almost never been directly investigated. There is therefore an important gap to be filled by studying how ALAN might affect the interactions between bats and their predators (e.g. roost monitoring by local associations could be used to investigate whether lit roosts are more prone to predation by owls, PAM could be used to evaluate simultaneously the presence of bats and their avian predators, etc.). Furthermore, it should not be forgotten that ALAN has been shown to have a wide range of effect on insects (Owens et al., 2019) and could then lead, at least locally, to population declines (Boyes et al., 2021; Owens et al., 2019). At the landscape scales, light pollution could therefore be responsible for an overall decline in food resources for bats.

Another biotic condition that may be modified by ALAN, but which has not received yet much attention, is competition. As a matter of fact, it might be hypothesised that narrow-space-foraging species might actually be deterred from foraging around light sources because of the high abundance of other species such as *Pipistrellus* spp. around them (Spoelstra et al., 2017). Arlettaz et al. (2000) also suggested that light pollution might provide immediate

benefits for abundant species able to forage near streetlights, which might be detrimental to others in the long term. ALAN might also increase competition for bats of the same foraging guild. Indeed, Salinas-Ramos et al. (2021) showed that while both *P. kuhlii* and *P. pipistrellus* showed a preference for light-polluted areas, these two species segregated habitats at a small spatial scale. In particular, the association of *P. pipistrellus* with ALAN was weakened by the presence of *P. kuhlii*. However, this study is one of the few to focus on the potential alteration of competition by ALAN, raising the need for further studies. For example, it could be interesting to assess whether the Vigie-Chiro dataset (**Box 3**) – which consists of simultaneous recordings of several species – could be used to further explore possible niche segregation between species in light-polluted landscapes.

2.3 Potential consequences for population dynamics

Overall, it appears that ALAN is having substantial impacts on both the biotic and abiotic environment of bats and might therefore create a set of conditions in which at least the populations of some bat species will not be able to persist. For narrow-space-foraging species, which have been shown to be negatively impacted by ALAN whatever the scale and behaviour under consideration, the straightforward hypothesis would be that light pollution could lead to a decrease in individual fitness and have cascading adverse effect on population dynamics (**Figure 31**). This prediction is fortified by studies showing that some narrow-space-foraging species (*Myotis* spp. and *Plecotus* spp.) are indeed less abundant in light-polluted landscapes than in dark landscapes (Barré et al., 2021b; Lewanzik et al., 2021) and a study that found that the colony size of *R. ferrumequinum* was lower in illuminated landscapes (Froidevaux et al., 2017).

For edge- and open-space-foraging species the effect of ALAN on population dynamics is more difficult to predict as light pollution appears to be beneficial in some contexts (e.g. by allowing them to forage on a predictable insect biomass around streetlights, however not always, see **Kerbiriou et al., (2020)**) while being detrimental in others (e.g. by reducing landscape connectivity (Hale et al., 2015; Laforge et al., 2019; **Pauwels et al., (in prep)** (**Box 7**)) or by delaying activity (**Mariton et al., 2022; Box 6**) (**Figure 31**).

At the landscape scale, several studies showed that for some edge- and open-space-foraging species (*P. kuhlii*, *P. pygmaeus*, *P. nathusii* at low light levels, *E. serotinus*, *N. leisleri*), abundance is higher in light-polluted landscapes (Barré et al., 2021b; Laforge et al., 2019; Mathews et al., 2015), suggesting that ALAN may indeed have a positive effect on

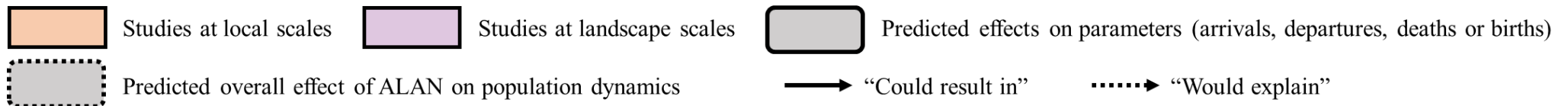
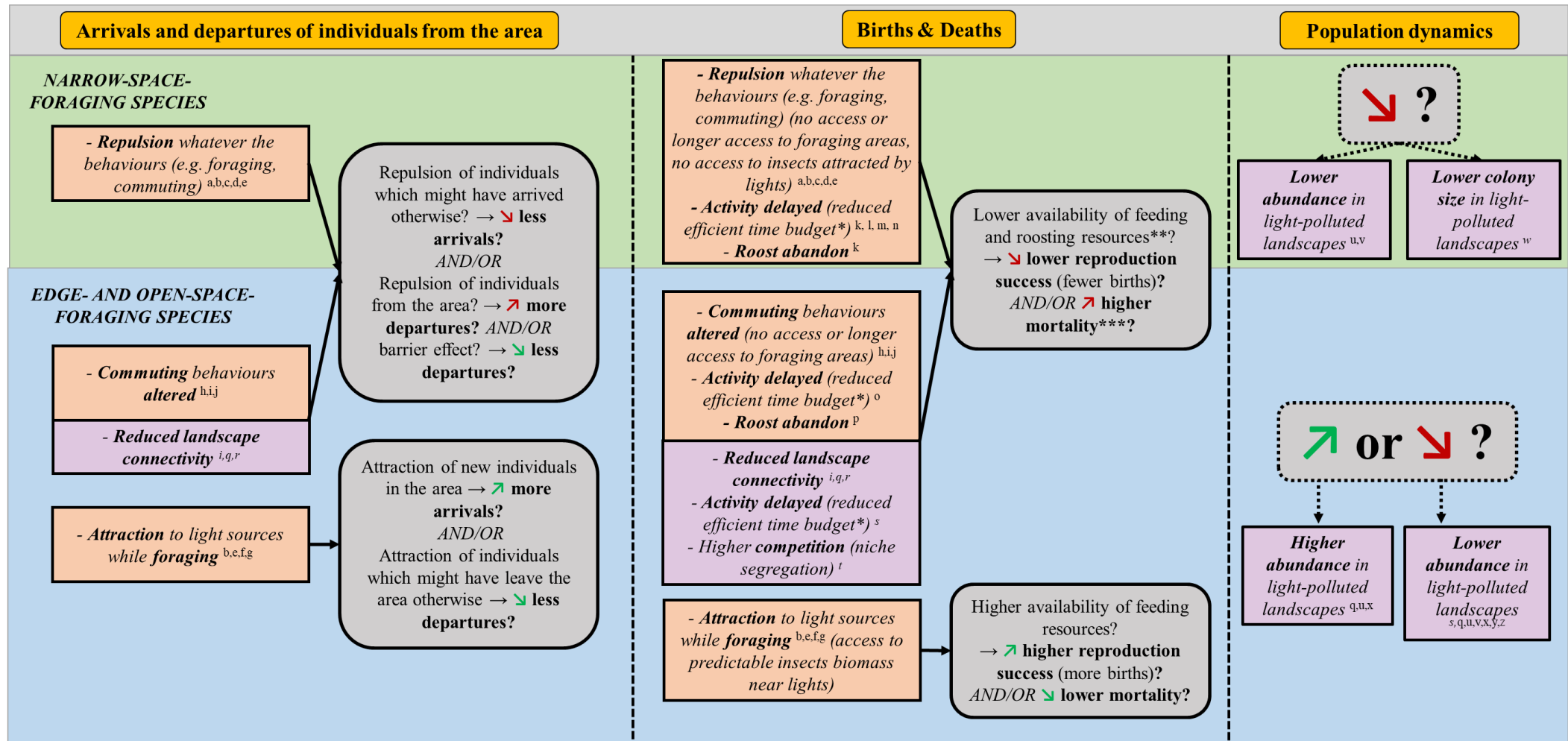
individual fitness and population dynamics in some contexts. However, these same studies and others, showed the opposite for other open- and edge-space-foraging species (*P. pipistrellus*, *P. kuhlii*, *E. serotinus*, *M. daubentonii*, *P. pygmaeus*, *P. nathusii*), with lower abundance in illuminated landscape (Azam et al., 2016; Barré et al., 2021b; Laforge et al., 2019; Lewanzik et al., 2021; **Mariton et al., 2022**; Mathews et al., 2015; **Box 6**). This suggests instead that ALAN may have a negative impact on individual fitness and population dynamics in some contexts. These inconsistent results for these two foraging guilds could have several explanations.

Firstly, as pointed out by Mathews et al., (2015) and Straka et al. (2019), the effects of light pollution on these species can be mediated by the amount of surrounding tree cover. Similarly, Barré et al. (2021b) showed that landscape composition could drive the response of bats to light pollution. Therefore, a better consideration of the interaction between ALAN and landscape parameters could help to understand these different effects of light pollution at the landscape scale on open- and edge-space-foraging species.

Secondly, while the “guild approach” based on foraging habits is useful for understanding and studying bat responses to light pollution, other functional traits of bats belonging to the same guilds may be heterogeneous (e.g. *E. serotinus* and *N. leisleri* belong to the same guild but show substantial differences in their diel activity pattern (**Mariton et al., (accepted)**), *Barbastellus barbastellus* and *M. daubentonii* are classified as edge-space-foraging species but they have a shorter echolocation range than most species in this guild (Voigt et al., 2021)), which could explain different responses to light pollution, raising the need to complement the guild approach with a species approach whenever possible .

Overall, the scientific literature on the impact of light pollution on bats is beginning to allow us to infer what the impact of ALAN on populations might be. The next step would therefore be to be able to measure directly this potential impact, which could be done thanks to datasets such as the one of the Vigie-Chiro program (initially designed to study bat species trends, **Box 3**) and large-scale data on light pollution such as the VIIRS satellite data which are now available annually (from 2012 to 2021) (Elvidge et al., 2021).

General discussion



* *Efficient time budget*: period during which bats may feed on the prey their diets are mainly composed of.

** *Lower feeding resources availability* might also occur because of declines in insect populations because of ALAN, in particular due to increased mortality near lights due to higher predation and exhaustion (Boyes et al., 2021; Owens et al., 2019).

*** *Higher mortality* could also occur because of ALAN effect on predation (by increasing the efficiency of predators relying on vision, by allowing diurnal predators to hunt at night), however it has never been shown.

Figure 31: Potential effects of ALAN on the population dynamics of bat species according to their guild.

^a (Lacoeuilhe et al., 2014), ^b (Rydell, 1992), ^c (Spoelstra et al., 2017), ^d (Voigt et al., 2021), ^e (Zeale et al., 2018), ^f (Azam et al., 2018), ^g (Stone et al., 2015a), ^h (Barré et al., 2020), ⁱ (Hale et al., 2015), ^j (Polak et al., 2011), ^k (Boldogh et al., 2007), ^l (Duvergé et al., 2000), ^m (Luo et al., 2021), ⁿ (McAney and Fairley, 1988), ^o (Haddock et al., 2019a), ^p (Arthur and Lemaire, 2015), ^q (Laforge et al., 2019), ^r (Pauwels et al. (*in prep*)), ^s (Mariton et al., 2022), ^t (Salinas-Ramos et al., 2021), ^u (Barré et al., 2021b), ^v (Lewanzik et al., 2021), ^w (Froidevaux et al., 2017), ^x (Mathews et al., 2015), ^y (Azam et al., 2016), ^z Box 6

2.4 Going beyond the model species

While the study of the impacts of light pollution on species and guilds is of utmost interest, the assessment of its impact on community structure and function remains an important issue. Due to the extent of light pollution and its different effects on different bat species, it could be assumed that ALAN would lead to a homogenisation of bat communities in favour of species with functional traits resulting in relatively low sensitivity to light pollution (either by allowing them to thrive in a light-polluted context or because of a great flexibility in the habitats and time periods they could exploit). However, to our knowledge, these possible impacts of ALAN on bat communities have almost never been studied. Besides studying how light pollution might affect taxonomic diversity (i.e. species richness and diversity), it would be of utmost importance to assess its effects on functional diversity (i.e. variability in ecological attributes) and phylogenetic diversity (i.e. evolutionary differences between species) as the former would allow to provides a mechanistic link to the resistance, resilience and functioning of ecosystems and the latter to assess the long-term evolutionary potential of the community in response to current and future modifications in the ecosystems (Cisneros et al., 2015; Laforge et al., 2022).

Furthermore, as knowledge of ALAN-mediated perturbations across a wide range of taxa continues to grow, there is a need for holistic approaches, integrating the whole trophic-chain and focusing on multiple spatiotemporal scales. For instance, we explained above that bats' responses to light pollution are likely to be strongly driven by the impacts of light pollution on their prey and predators both at the local scale (e.g. attraction/repulsion behaviour, possibility of increased predation efficiency of visual predators at the vicinity of lights) and at broader spatiotemporal scales (e.g. long-term reduction of insect populations in light-polluted landscapes, possible landscape scale mismatch between diel activity peak of bats and of their

prey). Assessing the relative importance of top-down (grazer-, parasite- and predator-controlled) and bottom-up effects (resource-controlled) of ALAN on different levels of trophic chains would then help to better understand the long-term impact of light pollution on species (e.g. by highlighting how disturbances at the lower and/or higher trophic level could have significant demographic impacts on the species studied) and to predict cascading alterations of ecosystem functions (Bennie et al., 2018).

3. Developing a multiscale and multidimensional approach to design mitigation measures and assess their effectiveness

Despite some remaining gaps in knowledge, the evidences on the impacts of light pollution on biodiversity are now overwhelming, hence the need to implement mitigation measures. While not lighting new areas (and by extension, removing light points) is obviously the most effective measure, other measures commonly cited in the literature are reducing the duration of lighting, reducing light trespass into areas that are not intended to be lit, reducing light intensity and modifying the emission spectrum (Gaston et al., 2012).

3.1. The need to better take into account the temporal dimension

The first two chapters of this PhD can be seen as a plea for a better consideration of the temporal dimension in mitigating the impacts of light pollution on biodiversity. As a reminder, living organisms have developed endogenous circadian rhythms entertained by exogenous influences (e.g. temperature, light-dark cycles) (Aschoff, 1989; Erkert, 1982). This allows them to occupy a given temporal niche and to coordinate their activity with that of other organisms with which they interact (e.g. conspecifics, predators, prey) (Aschoff, 1989; Erkert, 1982). Thus, perturbation of diel activity patterns could have dramatic cascading consequences for fitness. It is therefore of utmost importance to identify species whose diel activity patterns may be disrupted by anthropogenic pressures and to determine important times to preserve.

Firstly, it appears that a better integration of the temporal ecology of species should help to guide choices aimed at reducing the duration of lighting. In the field, this lever is mainly reflected in the adoption of the PNL, however, according to **Mariton et al. (accepted)**, in order to protect at least the late-emerging bats, which are among the most sensitive to light, the lights should be switched off earlier in the evening than what is done in most current PNL schemes.

Furthermore, as we showed in this PhD (**Kerbiriou et al., 2020; Mariton et al., 2022; Box 6; Box 7**), even early-emerging species that are usually considered to be “light tolerant” can be negatively affected by ALAN and should thus be protected from it. However, implementing a PNL scheme that would cover their range of activity would be almost equivalent to not switching on lights between sunset and sunrise, hence the need to find new ways of time-sharing between human light needs and non-human dark needs, such as on demand lighting (e.g. consisting in only switching on lights when movement is detected).

Interestingly, the effectiveness of PNL in mitigating the effect of ALAN on bats has so far only been assessed in terms of its ability to reduce the effect of light pollution on abundance (Azam et al., 2015; Hooker et al., 2022). Further studies should focus on assessing whether it could also mitigate the potential effect of ALAN on the disruption of bat diel activity patterns. More generally, even the effectiveness of the other most frequently cited mitigation measures (reduction of light intensity, improvement of lighting directivity and modification of emission spectrum) in reducing ALAN effect on biodiversity has rarely been assessed, in the field, in terms of their potential to mitigate disturbance of the diel temporal patterns of target species. For bats, at roost, Downs et al., (2003), suggested that the effect of ALAN on the onset of emergence may depend on the intensity and the emission spectrum. Red lights and low intensities appeared to be the least impactful choice, with light intensity being more important than colour in determining the onset of bat emergence. The results of **Mariton et al. (2022)** also suggest that light intensity may play an important role in the magnitude of the ALAN-induced activity delay, as even fine variations in light levels were detected to have an effect.

Furthermore, by showing that the skyglow probably contributed to the disruption of the diel activity patterns of bats, our results suggest that efforts to reduce the intensity of skyglow and its extent should not be neglected, firstly by reducing the number of light points and when this is not possible by limiting the intensity of the light and by directing light streams so that they do not shine above the horizontal. Therefore, the technological measures currently recommended to reduce the impacts of light pollution on biodiversity have the potential to reduce both the impact of ALAN on the spatial distribution of bats and their temporal distribution. However, the threshold for effectiveness as well as the relative importance of each of these measures could change depending on the dimension considered (time or space).

3.2. The need for multiscale approaches

Studying and understanding the effect of light pollution on biodiversity at various spatiotemporal scales seems to be an important prerequisite for producing recommendations. Studies conducted at the local scale, such as **Kerbiriou et al. (2020)**, can allow to identify and evaluate technological levers, those at the streetlight scale, that can contribute to reduce the impacts of ALAN on biodiversity. Indeed, they are valuable in understanding how ALAN can alter individual behaviours. However, it can be difficult to predict, from these studies, whether the observed individual behaviours may be detrimental, neutral or beneficial for bat populations at wider scales and in the long-term. For instance, based on **Kerbiriou et al. (2020)**, we could not predict whether the stronger attraction of bat species with increasing LED intensity was a positive or negative change in behaviour. Indeed, for instance, some individuals could benefit, in the short term, from the aggregation of insects around these lights, but this could also lead to a reduced food resource in the long term by inducing an over-mortality of insects attracted by the light sources (by exhaustion or predation).

Putting things into perspectives by considering larger scales (e.g. city scale as **Pauwels et al. (in prep)** (**Box 7**), national scale as **Mariton et al. (2022)**; **Box 6**) therefore seems to be a necessity. Indeed, focusing on the landscape scale is of utmost importance to assess the contribution to ALAN to habitat loss and fragmentation as well as to predict its long-term consequences on population dynamics (Azam et al., 2016; Gaston and Bennie, 2014).

Conducting wide scale surveys is a major challenge as it can be very costly and time-consuming. However, citizen science combined with technological developments (e.g. acoustic monitoring) offers great opportunities to monitor biodiversity at unprecedented spatial and temporal scales (Newson et al., 2015; van Klink et al., 2022). For instance, the citizen science program Vigie-Chiro (<https://www.vigienature.fr/fr/chauves-souris>, **Box 3**), whose data has been used in most of the studies presented in this PhD, has been active since 2006 and has approximately 600 participants, 16,000 sampled sites and 50,000 full nights of monitoring. It thus provides a formidable dataset to assess the impact of anthropogenic pressures on bats at wide spatiotemporal scales. Other bat monitoring programs, based on PAM and citizen science, in other countries, confirm the potential of these new monitoring approaches to provide a better understanding of large scale patterns in species' temporal and spatial distribution, abundance and their changes over time (Lewanzik et al., 2021; Newson et al., 2015; Roche et al., 2011). The use of citizen science coupled with PAM also opens up new perspectives for monitoring other taxa such as insects (van Klink et al., 2022). For instance, using the recordings made in

the framework of the Vigie-Chiro program, Jeliazkov et al. (2016) detected temporal decline of bush-crickets, thus demonstrating the potential of existing programs to open up to a greater diversity of taxa.

Assessing the effectiveness of mitigation measures to reduce the impact of ALAN on biodiversity is thus now possible. Although few studies have done so to date, Laforge et al. (2019) showed that reducing light intensity could improve landscape connectivity in urban areas for bats. In **Pauwels et al., (in prep)**, we showed that the transition to LEDs will decrease landscape connectivity even for a common “light tolerant” bat species. By predicting that improved light flux orientation or reduced light intensity may mitigate the effect of such a transition, we reaffirmed that, at the landscape scale, such technological levers could be effective.

Overall, these considerations raise the need to rethink the scale at which the mitigation measures should be implemented. Because ALAN contributes to landscape fragmentation and habitat loss and because of the diffuse nature of light pollution (which is characterised by a skyglow that can extend even far away from directly illuminated surfaces), there is a need to move from local mitigation measures to territorial planning. The concept of “dark ecological network” or “dark infrastructure” has thus emerged (Challéat et al., 2021; Sordello et al., 2022). It should aim to provide the darkness necessary, both in terms of space and duration, for species populations to survive in landscapes fragmented by light pollution, for instance by providing dark corridors between dark cores. At even wider scales, studies as **Mariton et al. (2022)** and the one presented in **Box 6**, which show an effect of light pollution on biodiversity at the scale of France, could help inform national policies.



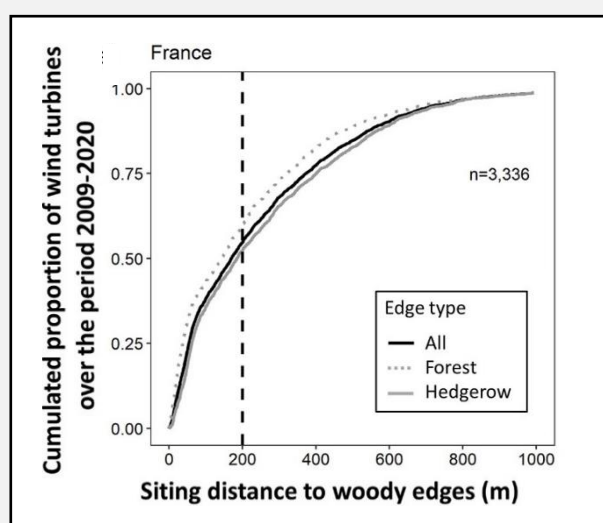
Box 8: Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: A call for action

Barré, K., Froidevaux, J.S.P., Leroux, C., **Mariton, L.**, Fritze, M., Kerbirou, C., Le Viol, I., Bas, Y., Roemer, C., 2022. Conservation Science and Practice 4, e12805. <https://doi.org/10.1111/csp2.12805>

In this study, we sought to assess the extent to which an international recommendation – based on the best available science and formulated as a precautionary principle – has been implemented in Europe. We focused on the **UNEP/EUROBATS agreement** which recommends, since 2008, to **site wind turbines at least 200 m away from woody edges** to reduce bat fatalities risks.

We focused on the three largest wind energy producers among the 37 countries that ratified this agreement: the United-Kingdom (UK), Germany and France. By assessing the siting distances between woody edges and wind turbines, we showed **that 61%, 78%, and 56%, respectively**, of the installed wind turbines **did not comply** with UNEP/EUROBATS guidelines, with no improvement over time.

We identified **possible causes** for these results and provided **recommendations for achieving better compliance**: (1) the implementation of the UNEP/EUROBATS guidelines in national legislative framework, (2) the updating of national and regional guidances to explicitly mention the recommendations made in the UNEP/EUROBATS guidelines, (3) the better notification of the environmental authorities and (4) the consideration of ecological impacts early in the planning process.



Cumulated proportion of wind turbines in operation since 2009 in relation to siting distance to woody edges in France. Vertical black dashed lines represent the minimum distance of wind turbine siting to woody edges according to the UNEP/EUROBATS guidelines (i.e. 200 m).

Source:

Barré et al., 2022 (CC BY 4.0)

4. Meeting the “real world’: The need for a transdisciplinary perspective

4.1. Translation of the scientific knowledge into practices

We acknowledge that translating knowledge such as those presented in this PhD into practice will face obstacles. Despite initiatives such as the *Conservation evidence database* (Sutherland et al., 2019), scientific evidences still frequently fail to filter through policies and guidance, for instance because of “circular referencing” (i.e. when an original guidance document references at least one other original guidance document) or the failure to incorporate new evidences into guidance (Hunter et al., 2021). Furthermore, even if scientific knowledge ends up being translated into legislation (e.g. the French order of 2018 on light pollution (*Arrêté du 27 décembre 2018*, 2018)) and recommendations (e.g. UNEP/EUROBATS guidelines), achieving compliance remains a major issue. When – as in Barré et al. (2022) study on the compliance of wind turbine installation to UNEP/EUROBATS guidelines (**Box 8**, Appendix V) – a low level of compliance is observed, it is necessary to question the obstacles that led to this situation and the levers that could be mobilised to change it.

4.2. From biological conservation to transdisciplinarity

In this PhD, we made recommendations for lighting management through the lens of conservation ecology. For us, the best light is the light that is not switched on, allowing darkness to reclaim its place in time and space. Thus, modifying the technical parameters of lighting (intensity, directivity, spectrum) can only be considered as a necessary measure to reduce the impacts of light pollution, but it cannot replace the removal of light points and the reduction of the duration of lighting.

However, these recommendations have to face with the “real world” whose interpretation requires a transdisciplinary approach in which, for instance, conservation biologists and wildlife managers have to interact with politicians and landscape planners (Battisti, 2003). Indeed, ALAN has not only ecological but also health and socio-cultural implications. The introduction of ALAN has its origins in the desire of humans to push back the darkness and to extend their activity at night. Thus, ALAN is a spatial planning tool that responds to various social uses such as architectural aesthetics, advertising, support for nocturnal economic activities, security and safety of people and goods (Challéat et al., 2021).

Interestingly, disentangling the actual benefits of ALAN on safety and security from the perceived ones is still a concern (Sánchez de Miguel et al., 2022). While some authors showed that ALAN does reduce night-time outdoor crimes (Chalfin et al., 2022; Painter, 1996; Welsh and Farrington, 2008), the adoption of LEDs and/or the implementation of mitigation measures (such as PNL and dimming) has not been linked to an increase in night-time road traffic collisions, crimes or thefts (Steinbach et al., 2015; Thompson et al., 2022). Dimming of lights has even been shown to tend to reduce crimes (Steinbach et al., 2015) while PNL schemes have been associated with a reduction in thefts from vehicles at night (Thompson et al., 2022).

Furthermore, it should not be forgotten that the environmental impact of ALAN is not restricted to its harmful impacts on biodiversity, it is also an energetic issue. Indeed, as a reminder, ALAN accounts for 16.5 % of the world's annual electricity production and for 5 % of global annual greenhouse gas emissions (1150 Mt of CO₂ per year) and could thus directly contribute to climate changes (Zissis et al., 2021). It is therefore a major issue in the current context of the need for an energy transition. By extension, it has also become an important financial issue, especially in light of the recent energy crisis. For instance, in France, ALAN is responsible for 41 % of the electricity consumption of municipalities and 37 % of their energy bill (Agence de la transition écologique — ADEME Expertises, n.d.).

In addition, indoor and outdoor ALAN has been associated with health issues in humans, including mental disorders (Chen et al., 2022; Tancredi et al., 2022), cancers (Lai et al., 2021) and obesity (Lai et al., 2020). Loss of darkness also alters cultural amenities (Challéat et al., 2021). For instance, by deteriorating darkness, it masks the starry sky (nowadays the Milky Way is hidden from more than a third of humanity (Falchi et al., 2016)). More generally, it deprives humans of a philosophical, touristic and artistic resource and disrupts their relationship with nature (Challéat et al., 2021).

As a consequence, light pollution mitigation is a complex issue that involves finding the best compromise between human needs and expectations for ALAN (e.g. improving quality of life, maintaining a high standard of living and nocturnal activities) and ecological, health and socio-cultural needs for darkness (Challéat et al., 2021; Franchomme et al., 2019). Overall, the shift from *“lighting where and when it is possible”* to the *“right way of lighting”* (e.g. providing only the light necessary and no more) is increasingly advocated for (Beaudet et al., 2022; Challéat et al., 2021).

Based on the observation that the main reluctance of local authorities to change lighting practices was a potential rejection by citizens, Beaudet et al. (2022) assessed the willingness of citizens to accept the transition to more environmentally-friendly lighting management.

They showed that citizens were generally open to changes toward more sustainable practices. Such results are consistent with previous studies showing a fairly broad public acceptance for the implementation of mitigation measures to reduce light pollution (Franchomme et al., 2019; Lyytimäki and Rinne, 2013; Silver and Hickey, 2020). In the study of Beaudet et al. (2022), the most accepted measure was to change to colour of the light. A late-starting PNL scheme (starting at 1 a.m.) also seemed to be a measure that can be implemented quite easily, whereas advancing the switch off to midnight met more resistance.

The study of Beaudet et al. (2022) was conducted in a French metropolis. In this country, local authorities' budget cuts and energy transition goals has led many municipalities to implement PNL and/or other mitigation measures (Challéat et al., 2021). However, these initiatives remain spatially scattered (Challéat et al., 2021). As we advocated in this PhD, from our point of view as conservation ecologists, light pollution reduction should not only be thought of at the local scale (e.g. streetlights or municipal scale), but also at the landscape or territorial scale. However, in France, public lighting is managed by default at the municipal level, and compliance with French regulations on light pollution is mainly the responsibility of mayors. Thus, there is a mismatch between the scales of ALAN management and those to be considered for biodiversity protection, particularly, with regard to the landscape fragmentation generated by light pollution. The fact that institutional management frameworks do not match the scale of ecological processes is not specific to light pollution and has been shown to be particularly pronounced in urban contexts (Borgström et al., 2006).

However, since the recognition in the Grenelle I law that ALAN can generate “*dangers or caus[e] excessive disturbance to people, fauna, flora or ecosystems*”, lead to “*energy waste*” and prevent “*observation of the night sky*” (LOI n° 2009-967 du 3 août 2009 de programmation relative à la mise en œuvre du Grenelle de l'environnement (1), 2009), France has developed a legislative package on light pollution and energy transition that wants to appear ambitious. The consideration of energy and environmental concerns related to ALAN is increasingly being incorporated into territorial planning and, in particular, in the Regional schemes for development, sustainable development and territorial equality (*Schémas régionaux d'aménagement, de développement durable et d'égalité des territoires*, SRADDET) (Lapostolle and Challéat, 2019). These schemes articulate the various territorial planning instruments at sub-regional levels, such as the territorial coherence schemes (*Schémas de cohérence territoriale*, SCoT) or the charters of the regional natural Parks (*Parcs naturels régionaux*, PNR) (Article L4251-3, n.d.; Lapostolle and Challéat, 2019).



Box 9: Transdisciplinary project: public lighting practices in the municipalities of the French regional nature Parks

Partnership:

Geography: Samuel Challéat (Researcher, UMR GÉODE), Olivia Gardella (intern, Université paris Cité) Johan Milian (Researcher, geography, UMR LADYSS)

Ecology: Léa Mariton (PhD student, UMR CESCO – supervisors: Christian Kerbiriou, Isabelle Le Viol).

This box is a synthesis of the work presented in Gardella (2022) (report) (Olivia Gardella's internship was supervised by Samuel Challéat, Léa Mariton and Johan Milian)

Context and objectives:

More than ten years after the first recognition of the negative effect of ALAN in French law (*LOI n° 2009-967 du 3 août 2009 de programmation relative à la mise en œuvre du Grenelle de l'environnement (1)*, 2009), it would be of utmost interest to have a panoptic vision on public lighting practices in municipalities, as well as to evaluate how such practices have emerged and been implemented. To do so, we chose to focus on municipalities located in particular French territories: the regional nature Parks (*Parcs naturels régionaux*, PNRs, 58 parks)

They are protected areas belonging to the category V of the IUCN protected areas management categories system. The main aim of the PNRs is to establish sustainable economic and social development, while preserving their landscape, natural and cultural heritage (Fédération des Parcs naturels régionaux, n.d.). A PNR is organised around a charter approved by the municipalities making up its territory. Therefore, the PNRs are key actors who could encourage their local partners to act on ALAN and support municipalities in their efforts to reduce light pollution.

We thus design a transdisciplinary project with the following objectives:

- (1) Carry out an assessment of the public lighting practices in municipalities located in PNRs. This assessment could then be used to compare actual practices with the current state of knowledge on the impact of light pollution on biodiversity.
- (2) To assess whether and to what extent territorial approaches have been able to initiate changes in practices. This knowledge could then help to understand what role scientific knowledge can play: does it contribute to debates, and if so, to changes in practices?

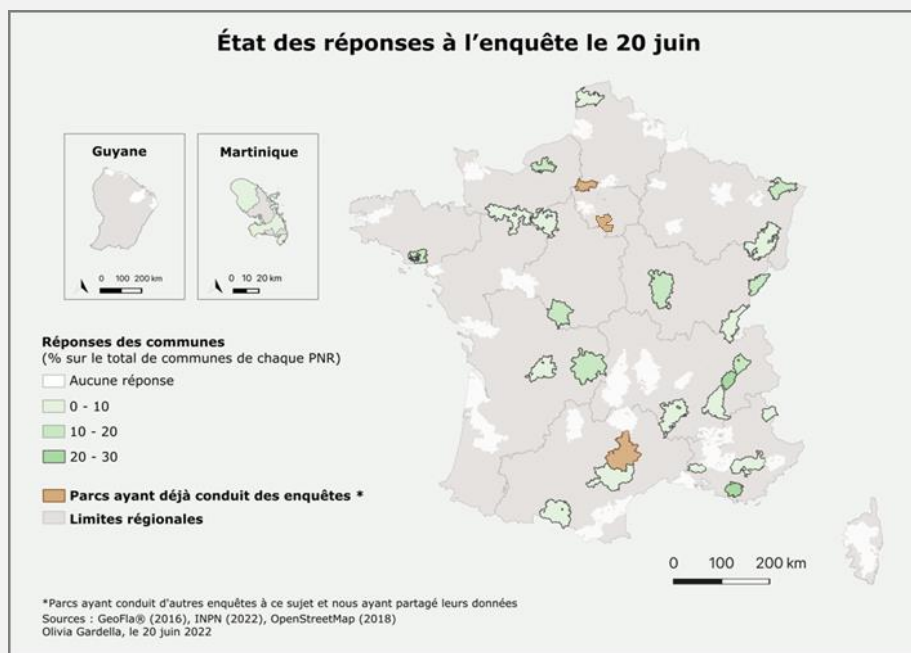


Box 9: Transdisciplinary project: public lighting practices in the municipalities of the French regional nature Parks

Material and methods:

Because this study was to be conducted at the national scale, we built an online survey on the LimeSurvey software (Limesurvey GmbH, n.d.). this survey was addressed to elected or employed members of municipalities. We tested a first version of this survey with the PNR du Morvan in the end of 2021. It helped us to improve the survey, the final form of which was constituted of four parts: “Your municipality” (general information on the respondent and the municipality he/she represents), “Your public lighting equipment” (technological information), “Your lighting practices” (PNL, dimming, etc.), “Your territorial approach” (actors interested in the nocturnal environment and their involvement in changing practices). Eventually, the survey consisted of 78 questions whose appearance depended on the previous answers. In its shortest version the survey was constituted of 21 questions and, in its longest version of 61 questions.

To disseminate this survey, we relied on the help of PNR project managers (*chargés de mission*) working on biodiversity or energy and the PNR directors, whom we asked to relay the survey to the municipalities in their territory. The survey was launched on 1 April 2022 and is still active, although reminders have not been sent since July to encourage municipalities to answer.



Rate of answers by PNR after the second reminding (204 answer).

Source: Gardella, 2022



Box 9: Transdisciplinary project: public lighting practices in the municipalities of the French regional nature Parks

Preliminary results and perspectives

To date, 227 full responses from almost half of the PNRs have been provided, most of which were collected between April and June 2022. We exchanged with three other PNRs that have already conducted surveys on lighting practices in their territories, and they agreed to share their data (mainly technological) with us. Eventually, three other parks did not wish to disseminate our survey because they did not want to over-solicit municipalities and/or as they feared that elected members would not be able to answer our questions.

Responses: *Indicate whether your municipality is currently engaged in one or more of these approaches to reduce ALAN*

Sources: Gardella, 2022

	Number	Percentage (in %)
Lighting on demand (SMS, application)	0	0
Unknow information	4	3
Presence detector	8	6
Currently, we do not practice any of these approaches	17	13
Removal of light points	18	14
Relamping with reduction of the installed power	28	22
Variation of light intensity	30	24
Part-night lighting	83	65

The first analyses of this survey were carried out on the results collected before May 16 2022, on 127 answers from municipalities in 20 PNRs. The municipalities represented in this first group of respondents correspond to municipalities that are mostly in direct management of their public lighting (50%) or that have delegated this responsibility to an energy syndicate (35%). The majority (84%) were involved in one or more ALAN reduction initiatives (see table above).

To the question: “*Let’s imagine you could do whatever you wanted. What do you think the ideal lighting park would be?*”, about half of the respondents (42 %) indicated that they would switch to LEDs while measures such as PNL or reduced intensity were much less mentioned. However, it should be kept in mind that many municipalities were already engaged in ALAN reduction measures, so they may not have mentioned them because they were already being implemented.



Box 9: Transdisciplinary project: public lighting practices in the municipalities of the French regional nature Parks

To the question: “*In your opinion, in your municipality, what are the benefits and/or drawbacks of reducing light pollution?*”, most respondents mentioned benefits. The most cited benefit (almost cited in 90% of the 87 answers to this a question) was energy savings, suggesting that energy and financial savings remain a main driver for changing lighting practices. Interestingly, the protection of biodiversity was cited in almost 60% of the responses, which suggest an awareness of ecological issues within these municipalities. Other benefits such as tourism or the protection of the starry sky were much less mentioned. About 25% of the respondents identified drawbacks, the main concerns being the security of the persons and goods and road safety.

The next step will be to carry out further analyses on the totality of the questions, the relationship between the answers and, if possible, the difference between PNRs. This could then allow us to determine, for example, whether territorial approaches are emerging (e.g. by assessing the potential driving role of the PNRs working on light pollution in changing the practices of their municipalities), what means have been implemented to bring about changes in practice (e.g. financing, possible triggers, actors involved, etc.), or to attempt to evaluate what part the preservation of the nocturnal environment plays in the debates. Another perspective could be to extend this questionnaire to municipalities outside the PNRs in order to evaluate the extent to which territorial practices and dynamics are different there.

The remaining challenges will then be to reach the threshold of answers allowing to conduct robust analyses and to integrate, when possible, data from surveys already conducted in PNRs. Another challenge will be to take into account the fact that this study was conducted at a very particular time, since it was released after the lock-downs and curfews due to the COVID-19 pandemic which led to a change in lighting practices in some French municipalities (in particular, temporary PNL schemes seem to have been adopted by municipalities during curfews) and during the current global energy crisis, which could conduct some municipalities to test PNL schemes to reduce expenditures.

French PNRs have a mission of experimentation and research that places them, potentially, at the forefront of the implementation of territorial approaches against anthropic pressures such as light pollution. Some of these PNRs have thus integrated specific actions to combat light pollution and to implement dark ecological networks (*trames noires*) (Busson and Carat, 2020), and have engaged in labelling procedures to enhance their work on the subject and to promote the quality of their night sky (e.g. International Dark Sky Reserves (International Dark-Sky Association, n.d.), Territoires de Villes et Villages étoilés (ANPCEN, 2021)).

However, the level of involvement of the PNRs on the issue of light pollution seems to vary. Thus, more than ten years after the inclusion of light pollution in the French legislative corpus, it seems necessary to assess communal lighting practices within these particular territories in France. Indeed, beyond the panoptic view that this could provide, it would also allow to highlight whether and to what extent territorial approaches have been at the origin of changes in practices. It would also allow us, as conservation biologists, to compare current practices with scientific knowledge on the impact of light pollution on biodiversity and to assess the extent to which the results of our research can contribute to debates and, possibly, to changes in practices. To answer these questions, we designed a transdisciplinary project in partnership with two geography researchers (Samuel Challéat – UMR GÉODE and Johan Milian – UMR LADYSS). The first phase of this project was developed by a geography intern (Olivia Gardella). The progress of this project, the first results obtained and the perspectives are presented in the **Box 9**. In particular, preliminary results tended to show that energy and financial savings remain a key driver for the evolution of lighting practices. It is therefore not surprising that municipalities have identified the transition to LEDs as one of the major steps towards an “ideal” lighting park. However, the protection of biodiversity also emerged in more than half of the responses analysed as a benefit of lighting reduction identified by municipalities.

More generally, because of the diffuse nature of light pollution, its extent and its wide range of negative effects on humans and non-humans, the need to act should no longer be limited to exceptional territories. To meet this challenge, dark ecological networks are essential tools, preserving both “remarkable” and “ordinary” biodiversity from light pollution. However, as advocated by Challéat et al., 2021 and as is now the case in some territories, dark ecological networks must go beyond the scientific concept to become action-oriented tools where the voice can be given back to the users of the territories.

General discussion

In conclusion, it is the current and future collaborations between scientists, landscape managers, citizens, politicians and associations that will be able to bring back the ancestral day-night alternation that gives rhythm to the lives of humans and non-humans.

Bibliography

General introduction

- Able, K.P., 1982. Skylight polarization patterns at dusk influence migratory orientation in birds. *Nature* 299, 550–551. <https://doi.org/10.1038/299550a0>
- Alaasam, V.J., Liu, X., Niu, Y., Habibian, J.S., Pieraut, S., Ferguson, B.S., Zhang, Y., Ouyang, J.Q., 2021. Effects of dim artificial light at night on locomotor activity, cardiovascular physiology, and circadian clock genes in a diurnal songbird. *Environmental Pollution* 282, 117036. <https://doi.org/10.1016/j.envpol.2021.117036>
- Amichai, E., Kronfeld-Schor, N., 2019. Artificial Light at Night Promotes Activity Throughout the Night in Nesting Common Swifts (*Apus apus*). *Sci Rep* 9, 11052. <https://doi.org/10.1038/s41598-019-47544-3>
- Ancillotto, L., Pafundi, D., Cappa, F., Chaverri, G., Gamba, M., Cervo, R., Russo, D., 2022. Bats mimic hymenopteran insect sounds to deter predators. *Current Biology* 32, R408–R409. <https://doi.org/10.1016/j.cub.2022.03.052>
- Appel, G., López-Baucells, A., Magnusson, W.E., Bobrowiec, P.E.D., 2017. Aerial insectivorous bat activity in relation to moonlight intensity. *Mammalian Biology* 85, 37–46. <https://doi.org/10.1016/j.mambio.2016.11.005>
- Arrêté du 27 décembre 2018 relatif à la prévention, à la réduction et à la limitation des nuisances lumineuses, 2018. , Journal officiel de la République française.
- Aschoff, J., 1989. Temporal orientation: circadian clocks in animals and humans. *Animal Behaviour* 37, 881–896. [https://doi.org/10.1016/0003-3472\(89\)90132-2](https://doi.org/10.1016/0003-3472(89)90132-2)
- Aubé, M., Roby, J., Kocifaj, M., 2013. Evaluating Potential Spectral Impacts of Various Artificial Lights on Melatonin Suppression, Photosynthesis, and Star Visibility. *PLoS ONE* 8, e67798. <https://doi.org/10.1371/journal.pone.0067798>
- Aulsebrook, A.E., Connelly, F., Johnsson, R.D., Jones, T.M., Mulder, R.A., Hall, M.L., Vyssotski, A.L., Lesku, J.A., 2020. White and Amber Light at Night Disrupt Sleep Physiology in Birds. *Current Biology* S0960982220309374. <https://doi.org/10.1016/j.cub.2020.06.085>
- Ayalon, I., Rosenberg, Y., Benichou, J.I.C., Campos, C.L.D., Sayco, S.L.G., Nada, M.A.L., Baquiran, J.I.P., Ligson, C.A., Avisar, D., Conaco, C., Kuechly, H.U., Kyba, C.C.M., Cabaitan, P.C., Levy, O., 2020. Coral Gametogenesis Collapse under Artificial Light Pollution. *Current Biology* S0960982220315827. <https://doi.org/10.1016/j.cub.2020.10.039>
- 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 Change Biol* 21, 4333–4341. <https://doi.org/10.1111/gcb.13036>
- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., Kerbiriou, C., 2018. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning* 175, 123–135. <https://doi.org/10.1016/j.landurbplan.2018.02.011>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., Kerbiriou, C., 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecol* 31, 2471–2483. <https://doi.org/10.1007/s10980-016-0417-3>

Bibliography

- Barber, J., Andersson, B., 1992. Too much of a good thing: light can be bad for photosynthesis. *Trends in Biochemical Sciences* 17, 61–66.
[https://doi.org/10.1016/0968-0004\(92\)90503-2](https://doi.org/10.1016/0968-0004(92)90503-2)
- Barré, K., Spoelstra, K., Bas, Y., Challéat, S., Ing, R.-K., Azam, C., Zissis, G., Lapostolle, D., Kerbirou, C., Le Viol, I., 2020. Artificial light may change flight patterns of bats near bridges along urban waterways. *Anim Conserv* acv.12635.
<https://doi.org/10.1111/acv.12635>
- 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>
- Becker, A., Whitfield, A.K., Cowley, P.D., Järnegren, J., Naesje, T.F., 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *J Appl Ecol* 50, 43–50.
<https://doi.org/10.1111/1365-2664.12024>
- Bedrosian, T.A., Fonken, L.K., Walton, J.C., Nelson, R.J., 2011. Chronic exposure to dim light at night suppresses immune responses in Siberian hamsters. *Biol. Lett.* 7, 468–471. <https://doi.org/10.1098/rsbl.2010.1108>
- Bennie, J., Davies, T.W., Cruse, D., Inger, R., Gaston, K.J., 2015. Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. *Phil. Trans. R. Soc. B* 370, 20140131.
<https://doi.org/10.1098/rstb.2014.0131>
- Bennie, J., Davies, T.W., Duffy, J.P., Inger, R., Gaston, K.J., 2014a. Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Sci Rep* 4, 3789. <https://doi.org/10.1038/srep03789>
- Bennie, J., Duffy, J.P., Inger, R., Gaston, K.J., 2014b. Biogeography of time partitioning in mammals. *Proc. Natl. Acad. Sci. U.S.A.* 111, 13727–13732.
<https://doi.org/10.1073/pnas.1216063110>
- Bird, B.L., Branch, L.C., Miller, D.L., 2004. Effects of Coastal Lighting on Foraging Behavior of Beach Mice. *Conservation Biology* 18, 1435–1439.
<https://doi.org/10.1111/j.1523-1739.2004.00349.x>
- Bird, S., Parker, J., 2014. Low levels of light pollution may block the ability of male glow-worms (*Lampyrus noctiluca* L.) to locate females. *J Insect Conserv* 18, 737–743.
<https://doi.org/10.1007/s10841-014-9664-2>
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)
- Bolliger, J., Haller, J., Wermelinger, B., Blum, S., Obrist, M.K., 2022. Contrasting impacts of street light shapes and LED color temperatures on nocturnal insects and bats. *Basic and Applied Ecology* S1439179122000615.
<https://doi.org/10.1016/j.baae.2022.07.002>
- Bolton, D., Mayer-Pinto, M., Clark, G.F., Dafforn, K.A., Brassil, W.A., Becker, A., Johnston, E.L., 2017. Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. *Science of The Total Environment* 576, 1–9.
<https://doi.org/10.1016/j.scitotenv.2016.10.037>
- Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., Pocock, M.J.O., 2021. Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* 7, eabi8322.
<https://doi.org/10.1126/sciadv.abi8322>
- Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., Pocock, M.J.O., 2020. Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle: Light pollution and moth life cycles. *Insect Conserv Divers* 14, 167–187.
<https://doi.org/10.1111/icad.12447>

Bibliography

- Bradshaw, W.E., Holzapfel, C.M., 2010a. Light, Time, and the Physiology of Biotic Response to Rapid Climate Change in Animals. *Annu. Rev. Physiol.* 72, 147–166. <https://doi.org/10.1146/annurev-physiol-021909-135837>
- Bradshaw, W.E., Holzapfel, C.M., 2010b. What Season Is It Anyway? Circadian Tracking vs. Photoperiodic Anticipation in Insects. *J Biol Rhythms* 25, 155–165. <https://doi.org/10.1177/0748730410365656>
- Bradshaw, W.E., Holzapfel, C.M., 2007. Evolution of Animal Photoperiodism. *Annu. Rev. Ecol. Evol. Syst.* 38, 1–25. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110115>
- Browning, E., Barlow, K.E., Burns, F., Hawkins, C., Boughey, K.L., 2021. Drivers of European bat population change: a review reveals evidence gaps. *Mam Rev* mam.12239. <https://doi.org/10.1111/mam.12239>
- Bumgarner, J.R., Nelson, R.J., 2021. Light at Night and Disrupted Circadian Rhythms Alter Physiology and Behavior. *Integrative and Comparative Biology* icab017. <https://doi.org/10.1093/icb/icab017>
- Camacho, L.F., Barragán, G., Espinosa, S., 2021. Local ecological knowledge reveals combined landscape effects of light pollution, habitat loss, and fragmentation on insect populations. *Biological Conservation* 262, 109311. <https://doi.org/10.1016/j.biocon.2021.109311>
- Challéat, S., Barré, K., Laforge, A., Lapostolle, D., Franchomme, M., Sirami, C., Le Viol, I., Milian, J., Kerbirou, C., 2021. Grasping darkness: the dark ecological network as a social-ecological framework to limit the impacts of light pollution on biodiversity. *E&S* 26, art15. <https://doi.org/10.5751/ES-12156-260115>
- Charbonnier, Y., Papura, D., Touzot, O., Rhouy, N., Sentenac, G., Rusch, A., 2021. Pest control services provided by bats in vineyard landscapes. *Agriculture, Ecosystems & Environment* 306, 107207. <https://doi.org/10.1016/j.agee.2020.107207>
- Chen, Y.-R., Wei, W.-L., Tzeng, D.T.W., Avalon, C.S.O., Tang, H.-C., Wu, C.-S., Lin, S.-S., Zhong, S., Yang, E.-C., 2021. Effects of artificial light at night (ALAN) on gene expression of *Aquatica ficta* firefly larvae. *Environmental Pollution* 116944. <https://doi.org/10.1016/j.envpol.2021.116944>
- Cieraad, E., van Grunsven, R.H.A., van der Sman, F., Zwart, N., Musters, Kees.J.M., Strange, E., van Langevelde, F., Trimbos, K.B., 2022. Lack of local adaptation of feeding and calling behaviours by *Yponomeuta cagnagellus* moths in response to artificial light at night. *Insect Conserv Diversity* icad.12568. <https://doi.org/10.1111/icad.12568>
- Cronin, A.D., Smit, J.A.H., Halfwerk, W., 2022. Anthropogenic noise and light alter temporal but not spatial breeding behavior in a wild frog. *Behavioral Ecology* arac077. <https://doi.org/10.1093/beheco/arac077>
- Czarnecka, M., Jermacz, Ł., Glazińska, P., Kulasek, M., Kobak, J., 2022. Artificial light at night (ALAN) affects behaviour, but does not change oxidative status in freshwater shredders. *Environmental Pollution* 306, 119476. <https://doi.org/10.1016/j.envpol.2022.119476>
- Da Silva, A., Valcu, M., Kempenaers, B., 2015. Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Phil. Trans. R. Soc. B* 370, 20140126. <https://doi.org/10.1098/rstb.2014.0126>
- Dacke, M., Byrne, M.J., Scholtz, C.H., Warrant, E.J., 2004. Lunar orientation in a beetle. *Proc. R. Soc. Lond. B* 271, 361–365. <https://doi.org/10.1098/rspb.2003.2594>
- Dacke, M., Nilsson, D.-E., Scholtz, C.H., Byrne, M., Warrant, E.J., 2003. Insect orientation to polarized moonlight. *Nature* 424, 33–33. <https://doi.org/10.1038/424033a>

Bibliography

- Davies, T.W., Bennie, J., Cruse, D., Blumgart, D., Inger, R., Gaston, K.J., 2017. Multiple night-time light-emitting diode lighting strategies impact grassland invertebrate assemblages. *Glob Change Biol* 23, 2641–2648. <https://doi.org/10.1111/gcb.13615>
- Davies, T.W., Bennie, J., Gaston, K.J., 2012. Street lighting changes the composition of invertebrate communities. *Biol. Lett.* 8, 764–767. <https://doi.org/10.1098/rsbl.2012.0216>
- Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for bat conservation: Part-night lighting and bats. *Anim Conserv* 18, 512–516. <https://doi.org/10.1111/acv.12200>
- de Jong, M., Ouyang, J.Q., Da Silva, A., van Grunsven, R.H.A., Kempenaers, B., Visser, M.E., Spoelstra, K., 2015. Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species. *Phil. Trans. R. Soc. B* 370, 20140128. <https://doi.org/10.1098/rstb.2014.0128>
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010. Defining and measuring ecological specialization. *Journal of Applied Ecology* 47, 15–25. <https://doi.org/10.1111/j.1365-2664.2009.01744.x>
- Dominoni, D.M., Borniger, J.C., Nelson, R.J., 2016. Light at night, clocks and health: from humans to wild organisms. *Biol. Lett.* 12, 20160015. <https://doi.org/10.1098/rsbl.2016.0015>
- Dominoni, D.M., de Jong, M., van Oers, K., O'Shaughnessy, P., Blackburn, G.J., Atema, E., Mateman, A.C., D'Amelio, P.B., Trost, L., Bellingham, M., Clark, J., Visser, M.E., Helm, B., 2022. Integrated molecular and behavioural data reveal deep circadian disruption in response to artificial light at night in male Great tits (*Parus major*). *Sci Rep* 12, 1553. <https://doi.org/10.1038/s41598-022-05059-4>
- Doucet, S.M., Meadows, M.G., 2009. Iridescence: a functional perspective. *J. R. Soc. Interface.* 6, S115–S132. <https://doi.org/10.1098/rsif.2008.0395.focus>
- Duarte, C., Quintanilla-Ahumada, D., Anguita, C., Manríquez, P.H., Widdicombe, S., Pulgar, J., Silva-Rodríguez, E.A., Miranda, C., Manríquez, K., Quijón, P.A., 2019. Artificial light pollution at night (ALAN) disrupts the distribution and circadian rhythm of a sandy beach isopod. *Environmental Pollution* 248, 565–573. <https://doi.org/10.1016/j.envpol.2019.02.037>
- Durrant, J., Michaelides, E.B., Rupasinghe, T., Tull, D., Green, M.P., Jones, T.M., 2015. Constant illumination reduces circulating melatonin and impairs immune function in the cricket *Teleogryllus commodus*. *PeerJ* 3, e1075. <https://doi.org/10.7717/peerj.1075>
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- Eisenbeis, G., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany, in: *Ecological Consequences of Artificial Night Lighting*. Washington DC, pp. 281–304.
- 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
- Evans, J.A., Elliott, J.A., Gorman, M.R., 2007. Circadian Effects of Light No Brighter Than Moonlight. *J Biol Rhythms* 22, 356–367. <https://doi.org/10.1177/0748730407301988>
- 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>

Bibliography

- Farnworth, B., Innes, J., Kelly, C., Littler, R., Waas, J.R., 2018. Photons and foraging: Artificial light at night generates avoidance behaviour in male, but not female, New Zealand weta. *Environmental Pollution* 236, 82–90. <https://doi.org/10.1016/j.envpol.2018.01.039>
- Farnworth, B., Innes, J., Waas, J.R., 2016. Converting Predation Cues into Conservation Tools: The Effect of Light on Mouse Foraging Behaviour. *PLoS ONE* 11, e0145432. <https://doi.org/10.1371/journal.pone.0145432>
- French-Constant, R.H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., McGregor, P.K., 2016. Light pollution is associated with earlier tree budburst across the United Kingdom. *Proc. R. Soc. B.* 283, 20160813. <https://doi.org/10.1098/rspb.2016.0813>
- Firebaugh, A., Haynes, K.J., 2016. Experimental tests of light-pollution impacts on nocturnal insect courtship and dispersal. *Oecologia* 182, 1203–1211. <https://doi.org/10.1007/s00442-016-3723-1>
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecol Biogeography* 16, 265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>
- Fonken, L.K., Aubrecht, T.G., Meléndez-Fernández, O.H., Weil, Z.M., Nelson, R.J., 2013. Dim Light at Night Disrupts Molecular Circadian Rhythms and Increases Body Weight. *J Biol Rhythms* 28, 262–271. <https://doi.org/10.1177/0748730413493862>
- Fonken, L.K., Workman, J.L., Walton, J.C., Weil, Z.M., Morris, J.S., Haim, A., Nelson, R.J., 2010. Light at night increases body mass by shifting the time of food intake. *Proc. Natl. Acad. Sci. U.S.A.* 107, 18664–18669. <https://doi.org/10.1073/pnas.1008734107>
- Foster, J.J., Smolka, J., Nilsson, D.-E., Dacke, M., 2018. How animals follow the stars. *Proc. R. Soc. B.* 285, 20172322. <https://doi.org/10.1098/rspb.2017.2322>
- Foster, J.J., Tocco, C., Smolka, J., Khaldy, L., Baird, E., Byrne, M.J., Nilsson, D.-E., Dacke, M., 2021. Light pollution forces a change in dung beetle orientation behavior. *Current Biology* 31, 3935–3942.e3. <https://doi.org/10.1016/j.cub.2021.06.038>
- Fyie, L.R., Gardiner, M.M., Meuti, M.E., 2021. Artificial light at night alters the seasonal responses of biting mosquitoes. *Journal of Insect Physiology* 129, 104194. <https://doi.org/10.1016/j.jinsphys.2021.104194>
- Gaston, K.J., Bennie, J., 2014. Demographic effects of artificial nighttime lighting on animal populations. *Environ. Rev.* 22, 323–330. <https://doi.org/10.1139/er-2014-0005>
- Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol Rev* 88, 912–927. <https://doi.org/10.1111/brv.12036>
- Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. REVIEW: Reducing the ecological consequences of night-time light pollution: options and developments. *J Appl Ecol* 49, 1256–1266. <https://doi.org/10.1111/j.1365-2664.2012.02212.x>
- Gaston, K.J., Davies, T.W., Nedelec, S.L., Holt, L.A., 2017. Impacts of Artificial Light at Night on Biological Timings. *Annu. Rev. Ecol. Evol. Syst.* 48, 49–68. <https://doi.org/10.1146/annurev-ecolsys-110316-022745>
- Gaston, K.J., Visser, M.E., Hölker, F., 2015. The biological impacts of artificial light at night: the research challenge. *Phil. Trans. R. Soc. B* 370, 20140133. <https://doi.org/10.1098/rstb.2014.0133>
- Geoffroy, M., Langbehn, T., Priou, P., Varpe, Ø., Johnsen, G., Le Bris, A., Fisher, J.A.D., Daase, M., McKee, D., Cohen, J., Berge, J., 2021. Pelagic organisms avoid white, blue, and red artificial light from scientific instruments. *Sci Rep* 11, 14941. <https://doi.org/10.1038/s41598-021-94355-6>

Bibliography

- Giavi, S., Fontaine, C., Knop, E., 2021. Impact of artificial light at night on diurnal plant-pollinator interactions. *Nat Commun* 12, 1690. <https://doi.org/10.1038/s41467-021-22011-8>
- Gomes, D.G.E., Appel, G., Barber, J.R., 2020. Time of night and moonlight structure vertical space use by insectivorous bats in a Neotropical rainforest: an acoustic monitoring study. *PeerJ* 8, e10591. <https://doi.org/10.7717/peerj.10591>
- Grubisic, M., van Grunsven, R.H.A., 2021. Artificial light at night disrupts species interactions and changes insect communities. *Current Opinion in Insect Science* S2214574521000717. <https://doi.org/10.1016/j.cois.2021.06.007>
- Grubisic, M., van Grunsven, R.H.A., Kyba, C.C.M., Manfrin, A., Hölker, F., 2018. Insect declines and agroecosystems: does light pollution matter?: Insect declines and agroecosystems. *Ann Appl Biol* 173, 180–189. <https://doi.org/10.1111/aab.12440>
- Guetté, A., Godet, L., Juigner, M., Robin, M., 2018. Worldwide increase in Artificial Light At Night around protected areas and within biodiversity hotspots. *Biological Conservation* 223, 97–103. <https://doi.org/10.1016/j.biocon.2018.04.018>
- Guido, M.E., Carpentieri, A.R., Garbarino-Pico, E., 2002. Circadian Phototransduction and the Regulation of Biological Rhythms. *Neurochemical Research* 27, 1473–1489. <https://doi.org/10.1023/A:1021696321391>
- Haddock, J.K., Threlfall, C.G., Law, B., Hochuli, D.F., 2019a. Light pollution at the urban forest edge negatively impacts insectivorous bats. *Biological Conservation* 236, 17–28. <https://doi.org/10.1016/j.biocon.2019.05.016>
- Haddock, J.K., Threlfall, C.G., Law, B., Hochuli, D.F., 2019b. Responses of insectivorous bats and nocturnal insects to local changes in street light technology: Insectivorous bats and street light technology. *Austral Ecology* 44, 1052–1064. <https://doi.org/10.1111/aec.12772>
- Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G., Sadler, J.P., 2015. The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Glob Change Biol* 21, 2467–2478. <https://doi.org/10.1111/gcb.12884>
- Halfwerk, W., Jerem, P., 2021. A Systematic Review of Research Investigating the Combined Ecological Impact of Anthropogenic Noise and Artificial Light at Night. *Front. Ecol. Evol.* 9, 765950. <https://doi.org/10.3389/fevo.2021.765950>
- Helm, B., Ben-Shlomo, R., Sheriff, M.J., Hut, R.A., Foster, R., Barnes, B.M., Dominoni, D., 2013. Annual rhythms that underlie phenology: biological time-keeping meets environmental change. *Proc. R. Soc. B.* 280, 20130016. <https://doi.org/10.1098/rspb.2013.0016>
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D., Hänel, A., Kappeler, P.M., Völker, S., Schwöpe, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C., Tockner, K., 2010a. The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy. *E&S* 15, 13. <https://doi.org/10.5751/ES-03685-150413>
- Hölker, F., Wolter, C., Perkin, E.K., Tockner, K., 2010b. Light pollution as a biodiversity threat. *Trends in Ecology & Evolution* 25, 681–682. <https://doi.org/10.1016/j.tree.2010.09.007>
- Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats. *Environmental Pollution* 307, 119552. <https://doi.org/10.1016/j.envpol.2022.119552>
- Hutchinson, G.E., 1957. Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22, 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>

Bibliography

- IUCN World Conservation Congress, 2021. 084 - Taking action to reduce light pollution [WWW Document]. IUCN World Conservation Congress 2020. URL <https://www.iucncongress2020.org/motion/084> (accessed 12.16.22).
- Jones, G., Jacobs, D.S., Kunz, T.H., Willig, M.R., Racey, P.A., 2009. Carpe noctem: the importance of bats as bioindicators. *Endang. Species. Res.* 8, 93–115. <https://doi.org/10.3354/esr00182>
- Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. B* 346, 445–455. <https://doi.org/10.1098/rstb.1994.0161>
- Kaniewska, P., Alon, S., Karako-Lampert, S., Hoegh-Guldberg, O., Levy, O., 2015. Signaling cascades and the importance of moonlight in coral broadcast mass spawning. *eLife* 4, e09991. <https://doi.org/10.7554/eLife.09991>
- Kehoe, R., Sanders, D., Van Veen, F.J.F., 2022. Towards a mechanistic understanding of the effects of artificial light at night on insect populations and communities. *Current Opinion in Insect Science* 100950. <https://doi.org/10.1016/j.cois.2022.100950>
- Kelley, J.L., Tatarnic, N.J., Schröder-Turk, G.E., Endler, J.A., Wilts, B.D., 2019. A Dynamic Optical Signal in a Nocturnal Moth. *Current Biology* 29, 2919–2925.e2. <https://doi.org/10.1016/j.cub.2019.07.005>
- Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., Valcu, M., 2010. Artificial Night Lighting Affects Dawn Song, Extra-Pair Siring Success, and Lay Date in Songbirds. *Current Biology* 20, 1735–1739. <https://doi.org/10.1016/j.cub.2010.08.028>
- Kerbiriou, C., Barré, K., Mariton, L., Pauwels, J., Zissis, G., Robert, A., Le Viol, I., 2020. Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of Bats. *Diversity* 12, 165. <https://doi.org/10.3390/d12040165>
- Kernbach, M.E., Cassone, V.M., Unnasch, T.R., Martin, L.B., 2020. Broad-spectrum light pollution suppresses melatonin and increases West Nile virus–induced mortality in House Sparrows (*Passer domesticus*). *The Condor* duaa018. <https://doi.org/10.1093/condor/duaa018>
- Khattar, G., Vaz, S., Pereira Braga, P.H., Macedo, M., da Silveira, L.F.L., 2022. Life history traits modulate the influence of environmental stressors on biodiversity: The case of fireflies, climate and artificial light at night. *Diversity and Distributions* ddi.13584. <https://doi.org/10.1111/ddi.13584>
- Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., Fontaine, C., 2017. Artificial light at night as a new threat to pollination. *Nature* 548, 206–209. <https://doi.org/10.1038/nature23288>
- Kolbe, J.J., Moniz, H.A., Lapiedra, O., Thawley, C.J., 2021. Bright lights, big city: an experimental assessment of short-term behavioral and performance effects of artificial light at night on *Anolis* lizards. *Urban Ecosyst.* <https://doi.org/10.1007/s11252-021-01098-3>
- Kolkert, H., Smith, R., Rader, R., Reid, N., 2020. Insectivorous bats foraging in cotton crop interiors is driven by moon illumination and insect abundance, but diversity benefits from woody vegetation cover. *Agriculture, Ecosystems & Environment* 302, 107068. <https://doi.org/10.1016/j.agee.2020.107068>
- Korpach, A.M., Garroway, C.J., Mills, A.M., von Zuben, V., Davy, C.M., Fraser, K.C., 2022. Urbanization and artificial light at night reduce the functional connectivity of migratory aerial habitat. *Ecography* e05581. <https://doi.org/10.1111/ecog.05581>
- Kronfeld-Schor, N., Dominoni, D., de la Iglesia, H., Levy, O., Herzog, E.D., Dayan, T., Helfrich-Forster, C., 2013. Chronobiology by moonlight. *Proc. R. Soc. B.* 280, 20123088. <https://doi.org/10.1098/rspb.2012.3088>

Bibliography

- Kühne, J.L., van Grunsven, R.H.A., Jechow, A., Hölker, F., 2021. Impact of different wavelengths of artificial light at night on phototaxis in aquatic insects. *Integrative and Comparative Biology* icab149. <https://doi.org/10.1093/icb/icab149>
- Kupprat, F., Hölker, F., Kloas, W., 2020. Can skyglow reduce nocturnal melatonin concentrations in Eurasian perch? *Environmental Pollution* 262, 114324. <https://doi.org/10.1016/j.envpol.2020.114324>
- Kyba, C.C.M., 2018. Is light pollution getting better or worse? *Nat Astron* 2, 267–269. <https://doi.org/10.1038/s41550-018-0402-7>
- 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., 2017a. 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., Mohar, A., Posch, T., 2017b. How bright is moonlight? *Astronomy & Geophysics* 58, 1.31-1.32. <https://doi.org/10.1093/astrogeo/atx025>
- Kyba, C.C.M., Ruhtz, T., Fischer, J., Hölker, F., 2011. Cloud Coverage Acts as an Amplifier for Ecological Light Pollution in Urban Ecosystems. *PLoS ONE* 6, e17307. <https://doi.org/10.1371/journal.pone.0017307>
- La Sorte, F.A., Horton, K.G., 2020. Seasonal variation in the effects of artificial light at night on the occurrence of nocturnally migrating birds in urban areas. *Environmental Pollution* 116085. <https://doi.org/10.1016/j.envpol.2020.116085>
- Lacoeuilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., Kerbiriou, C., 2014. The Influence of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. *PLoS ONE* 9, e103042. <https://doi.org/10.1371/journal.pone.0103042>
- Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbiriou, C., Fonderflick, J., Besnard, A., 2019. Reducing light pollution improves connectivity for bats in urban landscapes. *Landscape Ecol* 34, 793–809. <https://doi.org/10.1007/s10980-019-00803-0>
- Lapostolle, D., Challéat, S., 2020. Making Darkness a Place-Based Resource: How the Fight against Light Pollution Reconfigures Rural Areas in France. *Annals of the American Association of Geographers* 1–20. <https://doi.org/10.1080/24694452.2020.1747972>
- Last, K.S., Hobbs, L., Berge, J., Brierley, A.S., Cottier, F., 2016. Moonlight Drives Ocean-Scale Mass Vertical Migration of Zooplankton during the Arctic Winter. *Current Biology* 26, 244–251. <https://doi.org/10.1016/j.cub.2015.11.038>
- Le Tallec, T., Perret, M., Théry, M., 2013. Light Pollution Modifies the Expression of Daily Rhythms and Behavior Patterns in a Nocturnal Primate. *PLoS ONE* 8, e79250. <https://doi.org/10.1371/journal.pone.0079250>
- Le Tallec, T., Théry, M., Perret, M., 2015. Effects of light pollution on seasonal estrus and daily rhythms in a nocturnal primate. *JMAMMAL* 96, 438–445. <https://doi.org/10.1093/jmammal/gyv047>
- Lee, K.E.M., Lum, W.H.D., Coleman, J.L., 2021. Ecological impacts of the LED-streetlight retrofit on insectivorous bats in Singapore. *PLoS ONE* 16, e0247900. <https://doi.org/10.1371/journal.pone.0247900>
- Lewanzik, D., Voigt, C.C., 2017. Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *J Appl Ecol* 54, 264–271. <https://doi.org/10.1111/1365-2664.12758>
- Lewanzik, D., Voigt, C.C., 2014. Artificial light puts ecosystem services of frugivorous bats at risk. *J Appl Ecol* 51, 388–394. <https://doi.org/10.1111/1365-2664.12206>
- Lockett, M.T., Jones, T.M., Elgar, M.A., Gaston, K.J., Visser, M.E., Hopkins, G.R., 2021. Urban street lighting differentially affects community attributes of airborne and ground-dwelling invertebrate assemblages. *J Appl Ecol* 1365-2664.13969. <https://doi.org/10.1111/1365-2664.13969>

Bibliography

- Longcore, T., Rich, C., 2004. Ecological light pollution. *Frontiers in Ecology and the Environment* 2, 191–198. [https://doi.org/10.1890/1540-9295\(2004\)002\[0191:ELP\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2004)002[0191:ELP]2.0.CO;2)
- Luo, B., Xu, R., Li, Y., Zhou, W., Wang, W., Gao, H., Wang, Z., Deng, Y., Liu, Y., Feng, J., 2021. Artificial light reduces foraging opportunities in wild least horseshoe bats. *Environmental Pollution* 288, 117765. <https://doi.org/10.1016/j.envpol.2021.117765>
- Lynn, K.D., Quintanilla-Ahumada, D., Anguita, C., Widdicombe, S., Pulgar, J.M., Manríquez, P.H., Quijón, P.A., Duarte, C., 2021. Artificial light at night alters the activity and feeding behaviour of sandy beach amphipods and pose a threat to their ecological role in Atlantic Canada. *Science of The Total Environment* 780, 146568. <https://doi.org/10.1016/j.scitotenv.2021.146568>
- Mariton, L., Kerbirou, 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. *Environmental Pollution* 305, 119267. <https://doi.org/10.1016/j.envpol.2022.119267>
- Mariton, L., Le Viol, I., Bas, Y., Kerbirou, C., accepted. Characterising diel activity patterns to design conservation measures: case study of European bat species. *Biological Conservation*.
- McInerny, G.J., Etienne, R.S., 2012. Stitch the niche - a practical philosophy and visual schematic for the niche concept. *J. Biogeogr.* 39, 2103–2111. <https://doi.org/10.1111/jbi.12032>
- McMahon, O., Smyth, T., Davies, T.W., 2022. Broad spectrum artificial light at night increases the conspicuousness of camouflaged prey. *Journal of Applied Ecology*. <https://doi.org/10.1111/1365-2664.14146>
- McNaughton, E.J., Beggs, J.R., Gaston, K.J., Jones, D.N., Stanley, M.C., 2021. Retrofitting streetlights with LEDs has limited impacts on urban wildlife. *Biological Conservation* 254, 108944. <https://doi.org/10.1016/j.biocon.2020.108944>
- Meng, L., Zhou, Y., Román, M.O., Stokes, E.C., Wang, Z., Asrar, G.R., Mao, J., Richardson, A.D., Gu, L., Wang, Y., 2022. Artificial light at night: an under-appreciated effect on phenology of deciduous woody plants. *PNAS Nexus* pgac046. <https://doi.org/10.1093/pnasnexus/pgac046>
- Meyer-Rochow, V.B., 2007. Glowworms: a review of *Arachnocampa* spp. and kin. *Luminescence* 22, 251–265. <https://doi.org/10.1002/bio.955>
- Mickleburgh, S.P., Hutson, A.M., Racey, P.A., 2002. A review of the global conservation status of bats. *Oryx* 36, 18–34. <https://doi.org/10.1017/S0030605302000054>
- Miller, C.R., Barton, B.T., Zhu, L., Radeloff, V.C., Oliver, K.M., Harmon, J.P., Ives, A.R., 2017. Combined effects of night warming and light pollution on predator–prey interactions. *Proc. R. Soc. B.* 284, 20171195. <https://doi.org/10.1098/rspb.2017.1195>
- Miller, M.W., 2006. Apparent Effects of Light Pollution on Singing Behavior of American Robins. *The Condor* 108, 130–139. <https://doi.org/10.1093/condor/108.1.130>
- Mills, A.M., 2008. Latitudinal gradients of biologically useful semi-darkness. *Ecography* 31, 578–582. <https://doi.org/10.1111/j.0906-7590.2008.05346.x>
- Minnaar, C., Boyles, J.G., Minnaar, I.A., Sole, C.L., McKechnie, A.E., 2015. Stacking the odds: light pollution may shift the balance in an ancient predator-prey arms race. *J Appl Ecol* 52, 522–531. <https://doi.org/10.1111/1365-2664.12381>
- Mukai, A., Yamaguchi, K., Goto, S.G., 2021. Urban warming and artificial light alter dormancy in the flesh fly. *R. Soc. open sci.* 8, 210866. <https://doi.org/10.1098/rsos.210866>

Bibliography

- Negro, J.J., Bustamante, J., Melguizo, C., Ruiz, J.L., Grande, J.M., 2000. Nocturnal activity of lesser kestrels under artificial lighting conditions in Seville, Spain. *Journal of Raptor Research* 34, 327–329.
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>
- Owens, A.C.S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E.K., Seymoure, B.M., 2019. Light pollution is a driver of insect declines. *Biological Conservation* 241, 108259. <https://doi.org/10.1016/j.biocon.2019.108259>
- 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>
- Owens, A.C.S., Meyer-Rochow, V.B., Yang, E.-C., 2018. Short- and mid-wavelength artificial light influences the flash signals of *Aquatica ficta* fireflies (Coleoptera: Lampyridae). *PLoS ONE* 13, e0191576. <https://doi.org/10.1371/journal.pone.0191576>
- Papi, F., Pardi, L., 1963. On the lunar orientation of sandhoppers (Amphipoda talitridae). *The Biological Bulletin* 124, 97–105. <https://doi.org/10.2307/1539571>
- Parkinson, E., Lawson, J., Tiegs, S.D., 2020. Artificial light at night at the terrestrial-aquatic interface: Effects on predators and fluxes of insect prey. *PLoS ONE* 15, e0240138. <https://doi.org/10.1371/journal.pone.0240138>
- Parlin, A.F., Stratton, S.M., Guerra, P.A., 2022. Oriented migratory flight at night: Consequences of nighttime light pollution for monarch butterflies. *iScience* 25, 104310. <https://doi.org/10.1016/j.isci.2022.104310>
- Pauwels, J., Le Viol, I., Mariton, L., Laforge, A., Bas, Y., Coulon, A., Valet, N., Besnard, A., Fonderflick, J., Kerbirou, C., in prep. Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas.
- Pawson, S.M., Bader, M.K.-F., 2014. LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications* 24, 1561–1568. <https://doi.org/10.1890/14-0468.1>
- Polak, T., Korine, C., Yair, S., Holderied, M.W., 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert: Light pollution in deserts and bat foraging. *Journal of Zoology*. <https://doi.org/10.1111/j.1469-7998.2011.00808.x>
- Poot, H., Ens, B.J., de Vries, H., Donners, M.A.H., Wernand, M.R., Marquenie, J.M., 2008. Green Light for Nocturnally Migrating Birds. *E&S* 13, art47. <https://doi.org/10.5751/ES-02720-130247>
- R Core Team, 2022. R: A language and environment for statistical computing.
- Riegel, K.W., 1973. Light Pollution: Outdoor lighting is a growing threat to astronomy. *Science* 179, 1285–1291. <https://doi.org/10.1126/science.179.4080.1285>
- Rodríguez, A., Orozco-Valor, P.M., Sarasola, J.H., 2020. Artificial light at night as a driver of urban colonization by an avian predator. *Landscape Ecol.* <https://doi.org/10.1007/s10980-020-01132-3>
- Rotics, S., Dayan, T., Kronfeld-Schor, N., 2011. Effect of artificial night lighting on temporally partitioned spiny mice. *Journal of Mammalogy* 92, 159–168. <https://doi.org/10.1644/10-MAMM-A-112.1>
- Rowse, E.G., Harris, S., Jones, G., 2016. The Switch from Low-Pressure Sodium to Light Emitting Diodes Does Not Affect Bat Activity at Street Lights. *PLoS ONE* 11, e0150884. <https://doi.org/10.1371/journal.pone.0150884>

Bibliography

- Russo, D., Salinas-Ramos, V.B., Cistrone, L., Smeraldo, S., Bosso, L., Ancillotto, L., 2021. Do We Need to Use Bats as Bioindicators? *Biology* 10, 693. <https://doi.org/10.3390/biology10080693>
- Rydell, J., 1992. Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology* 6, 744–750. <https://doi.org/10.2307/2389972>
- Rydell, J., Entwistle, A.C., 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>
- Saigusa, M., 1980. Entrainment of a semilunar rhythm by a simulated moonlight cycle in the terrestrial crab, *Sesarma haematocheir*. *Oecologia* 46, 38–44. <https://doi.org/10.1007/BF00346963>
- Saldaña-Vázquez, R.A., Munguía-Rosas, M.A., 2013. Lunar phobia in bats and its ecological correlates: A meta-analysis. *Mammalian Biology* 78, 216–219. <https://doi.org/10.1016/j.mambio.2012.08.004>
- Salinas-Ramos, V.B., Ancillotto, L., Cistrone, L., Natasi, C., Bosso, L., Smeraldo, S., Sánchez-Cordero, V., Russo, D., 2021. Artificial illumination influences niche segregation in bats. *Environmental Pollution* 284, 117187. <https://doi.org/10.1016/j.envpol.2021.117187>
- Salmon, M., Tolbert, M.G., Painter, D.P., Goff, M., Reiners, R., 1995. Behavior of Loggerhead Sea Turtles on an Urban Beach. II. Hatchling Orientation. *Journal of Herpetology* 29, 568. <https://doi.org/10.2307/1564740>
- Sánchez de Miguel, A., Bennie, J., Rosenfeld, E., Dzurjak, S., Gaston, K.J., 2022. Environmental risks from artificial nighttime lighting widespread and increasing across Europe. *Sci. Adv.* 8, eabl6891. <https://doi.org/10.1126/sciadv.abl6891>
- Secondi, J., Mondy, N., Gippet, J.M.W., Touzot, M., Gardette, V., Guillard, L., Lengagne, T., 2021. Artificial light at night alters activity, body mass, and corticosterone level in a tropical anuran. *Behavioral Ecology* arab044. <https://doi.org/10.1093/beheco/arab044>
- Senzaki, M., Barber, J.R., Phillips, J.N., Carter, N.H., Cooper, C.B., Ditmer, M.A., Frstrup, K.M., McClure, C.J.W., Mennitt, D.J., Tyrrell, L.P., Vukomanovic, J., Wilson, A.A., Francis, C.D., 2020. Sensory pollutants alter bird phenology and fitness across a continent. *Nature*. <https://doi.org/10.1038/s41586-020-2903-7>
- Smit, J.A.H., Cronin, A.D., van der Wiel, I., Oteman, B., Ellers, J., Halfwerk, W., 2022. Interactive and independent effects of light and noise pollution on sexual signaling in frogs. *Front. Ecol. Evol.* 10, 934661. <https://doi.org/10.3389/fevo.2022.934661>
- Smith, R.A., Gagné, M., Fraser, K.C., 2020. Pre-migration artificial light at night advances the spring migration timing of a trans-hemispheric migratory songbird. *Environmental Pollution* 116136. <https://doi.org/10.1016/j.envpol.2020.116136>
- Somers-Yeates, R., Hodgson, D., McGregor, P.K., Spalding, A., French-Constant, R.H., 2013. Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biol. Lett.* 9, 20130376. <https://doi.org/10.1098/rsbl.2013.0376>
- 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.* 284, 20170075. <https://doi.org/10.1098/rspb.2017.0075>
- Stone, E.L., Harris, S., Jones, G., 2015a. Impacts of artificial lighting on bats: a review of challenges and solutions. *Mammalian Biology* 80, 213–219. <https://doi.org/10.1016/j.mambio.2015.02.004>
- Stone, E.L., Jones, G., Harris, S., 2009. Street Lighting Disturbs Commuting Bats. *Current Biology* 19, 1123–1127. <https://doi.org/10.1016/j.cub.2009.05.058>

Bibliography

- Stone, E.L., Wakefield, A., Harris, S., Jones, G., 2015b. The impacts of new street light technologies: experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide. *Phil. Trans. R. Soc. B* 370, 20140127. <https://doi.org/10.1098/rstb.2014.0127>
- Straka, T.M., Greif, S., Schultz, S., Goerlitz, H.R., Voigt, C.C., 2020. The effect of cave illumination on bats. *Global Ecology and Conservation* 21, e00808. <https://doi.org/10.1016/j.gecco.2019.e00808>
- Straka, T.M., Wolf, M., Gras, P., Buchholz, S., Voigt, C.C., 2019. Tree Cover Mediates the Effect of Artificial Light on Urban Bats. *Front. Ecol. Evol.* 7, 91. <https://doi.org/10.3389/fevo.2019.00091>
- Svensson, A.M., Rydell, J., 1998. Mercury vapour lamps interfere with the bat defence of tympanate moths (*Operophtera* spp.; Geometridae). *Animal Behaviour* 55, 223–226. <https://doi.org/10.1006/anbe.1997.0590>
- Syposz, M., Padget, O., Willis, J., Van Doren, B.M., Gillies, N., Fayet, A.L., Wood, M.J., Alejo, A., Guilford, T., 2021. Avoidance of different durations, colours and intensities of artificial light by adult seabirds. *Sci Rep* 11, 18941. <https://doi.org/10.1038/s41598-021-97986-x>
- Taylor, L.A., Thawley, C.J., Pertuit, O.R., Dennis, A.J., Carson, I.R., Tang, C., Johnson, M.A., 2022. Artificial light at night alters diurnal and nocturnal behavior and physiology in green anole lizards. *Physiology & Behavior* 257, 113992. <https://doi.org/10.1016/j.physbeh.2022.113992>
- The European Parliament and the Council of the European Union, 2009. Directive 2009/125/EC of the European Parliament and of the Council of 21 October 2009 establishing a framework for the setting of ecodesign requirements for energy-related products., *Official Journal of the European Union*.
- Torres, D., Tidau, S., Jenkins, S., Davies, T.W., 2020. Artificial skyglow disrupts celestial migration at night. *Current Biology* 30, R696–R697. <https://doi.org/10.1016/j.cub.2020.05.002>
- Touzot, M., Lefebvre, T., Lengagne, T., Secondi, J., Dumet, A., Konecny-Dupre, L., Veber, P., Navratil, V., Duchamp, C., Mondy, N., 2021. Transcriptome-wide deregulation of gene expression by artificial light at night in tadpoles of common toads. *Science of The Total Environment* 151734. <https://doi.org/10.1016/j.scitotenv.2021.151734>
- Van Doren, B.M., Horton, K.G., Dokter, A.M., Klinck, H., Elbin, S.B., Farnsworth, A., 2017. High-intensity urban light installation dramatically alters nocturnal bird migration. *Proc Natl Acad Sci USA* 114, 11175–11180. <https://doi.org/10.1073/pnas.1708574114>
- van Grunsven, R.H.A., van Deijk, J.R., Donners, M., Berendse, F., Visser, M.E., Veenendaal, E.M., Spoelstra, K., 2020. Experimental light at night has a negative long-term impact on macro-moth populations. *Current Biology* 30, R694–R695. <https://doi.org/10.1016/j.cub.2020.04.083>
- van Hasselt, S.J., Hut, R.A., Allocca, G., Vyssotski, A.L., Piersma, T., Rattenborg, N.C., Meerlo, P., 2021. Cloud cover amplifies the sleep-suppressing effect of artificial light at night in geese. *Environmental Pollution* 273, 116444. <https://doi.org/10.1016/j.envpol.2021.116444>
- Van Tichelen, P., Geerken, T., Jansen, B., Vanden Bosch, M., Van Hoof, V., Vanhooydonck, L., Vercalsteren, A., 2007. Final report lot 9: Public street lighting.
- Voigt, C.C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens, H.J.G.A., Mathews, F., Rydell, J., Spoelstra, K., Zagmajster, M., 2021. The Impact Of Light Pollution On Bats Varies According To Foraging Guild And Habitat Context. *BioScience* 71, 1103–1109. <https://doi.org/10.1093/biosci/biab087>

Bibliography

- Wakefield, A., Stone, E.L., Jones, G., Harris, S., 2015. Light-emitting diode street lights reduce last-ditch evasive manoeuvres by moths to bat echolocation calls. *R. Soc. open sci.* 2, 150291. <https://doi.org/10.1098/rsos.150291>
- Wang, J.-S., Tuanmu, M.-N., Hung, C.-M., 2021. Effects of artificial light at night on the nest-site selection, reproductive success and behavior of a synanthropic bird. *Environmental Pollution* 288, 117805. <https://doi.org/10.1016/j.envpol.2021.117805>
- West, K.E., Jablonski, M.R., Warfield, B., Cecil, K.S., James, M., Ayers, M.A., Maida, J., Bowen, C., Sliney, D.H., Rollag, M.D., Hanifin, J.P., Brainard, G.C., 2011. Blue light from light-emitting diodes elicits a dose-dependent suppression of melatonin in humans. *Journal of Applied Physiology* 110, 619–626. <https://doi.org/10.1152/japplphysiol.01413.2009>
- Wilson, A.A., Ditmer, M.A., Barber, J.R., Carter, N.H., Miller, E.T., Tyrrell, L.P., Francis, C.D., 2021. Artificial night light and anthropogenic noise interact to influence bird abundance over a continental scale. *Glob Change Biol* gcb.15663. <https://doi.org/10.1111/gcb.15663>
- 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 Change Biol* 24, 5909–5918. <https://doi.org/10.1111/gcb.14462>
- Zissis, G., Bertoldi, P., Serrenho, T., 2021. Update on the status of LED-lighting world market since 2018 (JRC Technical Report No. EUR 30500 EN). Publications Office of the European Union, Luxembourg.

Chapter 1 : Taking diel activity patterns into account in conservation measures

(Context and Perspectives)

- 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 Change Biol* 21, 4333–4341. <https://doi.org/10.1111/gcb.13036>
- Bennie, J., Davies, T.W., Duffy, J.P., Inger, R., Gaston, K.J., 2014. Contrasting trends in light pollution across Europe based on satellite observed night time lights. *Sci Rep* 4, 3789. <https://doi.org/10.1038/srep03789>
- Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for bat conservation: Part-night lighting and bats. *Anim Conserv* 18, 512–516. <https://doi.org/10.1111/acv.12200>
- 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
- Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol Rev* 88, 912–927. <https://doi.org/10.1111/brv.12036>
- Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats. *Environmental Pollution* 307, 119552. <https://doi.org/10.1016/j.envpol.2022.119552>
- Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. B* 346, 445–455. <https://doi.org/10.1098/rstb.1994.0161>
- Lindenmayer, D., Hunter, M., 2010. Some Guiding Concepts for Conservation Biology. *Conservation Biology* 24, 1459–1468. <https://doi.org/10.1111/j.1523-1739.2010.01544.x>
- Mariton, L., Le Viol, I., Bas, Y., Kerbiriou, C., accepted. Characterising diel activity patterns to design conservation measures: case study of European bat species. *Biological Conservation*.
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>
- Racey, P.A., Speakman, J.R., 1987. The energy costs of pregnancy and lactation in heterothermic bats. *Symp. zool. Soc. Lond.* 107–125.
- Robinson, M.F., Stebbings, R.E., 1997. Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *Journal of Zoology* 243, 117–136. <https://doi.org/10.1111/j.1469-7998.1997.tb05759.x>
- Rydell, J., 1992. Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology* 6, 744–750. <https://doi.org/10.2307/2389972>
- Swift, S.M., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology* 190, 285–295. <https://doi.org/10.1111/j.1469-7998.1980.tb01428.x>
- UICN France, MNHN, SFEPM, ONCFS, 2017. La Liste rouge des espèces menacées en France – Chapitre Mammifères de France métropolitaine. Paris, France.

Chapter 2: Impact of light pollution on bat diel activity patterns (Context and Perspectives)

- Arthur, L., Lemaire, M., 2015. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope ; Museum national d'Histoire Naturelle, Mèze; Paris.
- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., Kerbiriou, C., 2018. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning* 175, 123–135. <https://doi.org/10.1016/j.landurbplan.2018.02.011>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., Kerbiriou, C., 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecol* 31, 2471–2483. <https://doi.org/10.1007/s10980-016-0417-3>
- Barré, K., Vernet, A., Azam, C., Le Viol, I., Dumont, A., Deana, T., Vincent, S., Challéat, S., Kerbiriou, C., 2021. Landscape composition drives the impacts of artificial light at night on insectivorous bats. *Environmental Pollution* 292, 118394. <https://doi.org/10.1016/j.envpol.2021.118394>
- Bas, Y., Roemer, C., Julien, J.-F., 2020. Bat population trends [WWW Document]. Team-Chiro. URL <https://croemer3.wixsite.com/teamchiro/population-trends?lang=fr> (accessed 9.30.21).
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)
- Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., Pocock, M.J.O., 2021. Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* 7, eabi8322. <https://doi.org/10.1126/sciadv.abi8322>
- Catto, C.M.C., Racey, P.A., Stephenson, P.J., 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology* 235, 635–644. <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>
- Claireau, F., Bas, Y., Puechmaille, S.J., Julien, J., Allegrini, B., Kerbiriou, C., 2019. Bat overpasses: An insufficient solution to restore habitat connectivity across roads. *J Appl Ecol* 56, 573–584. <https://doi.org/10.1111/1365-2664.13288>
- Deverchère, P., Vauclair, S., Bosch, G., Moulherat, S., Cornuau, J.H., 2022. Towards an absolute light pollution indicator. *Sci Rep* 12, 17050. <https://doi.org/10.1038/s41598-022-21460-5>
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- Haddock, J.K., Threlfall, C.G., Law, B., Hochuli, D.F., 2019. Responses of insectivorous bats and nocturnal insects to local changes in street light technology: Insectivorous bats and street light technology. *Austral Ecology* 44, 1052–1064. <https://doi.org/10.1111/aec.12772>
- Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G., Sadler, J.P., 2015. The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Glob Change Biol* 21, 2467–2478. <https://doi.org/10.1111/gcb.12884>
- Hänel, A., Posch, T., Ribas, S.J., Aubé, M., Duriscoe, D., Jechow, A., Kollath, Z., Lolkema, D.E., Moore, C., Schmidt, N., Spoelstra, H., Wuchterl, G., Kyba, C.C.M., 2018. Measuring night sky brightness: methods and challenges. *Journal of Quantitative*

- Spectroscopy and Radiative Transfer 205, 278–290.
<https://doi.org/10.1016/j.jqsrt.2017.09.008>
- Hölker, F., Bolliger, J., Davies, T.W., Giavi, S., Jechow, A., Kalinkat, G., Longcore, T., Spoelstra, K., Tidau, S., Visser, M.E., Knop, E., 2021. 11 Pressing Research Questions on How Light Pollution Affects Biodiversity. *Front. Ecol. Evol.* 9, 767177. <https://doi.org/10.3389/fevo.2021.767177>
- Jechow, A., Kolláth, Z., Ribas, S.J., Spoelstra, H., Hölker, F., Kyba, C.C.M., 2017. Imaging and mapping the impact of clouds on skyglow with all-sky photometry. *Sci Rep* 7, 6741. <https://doi.org/10.1038/s41598-017-06998-z>
- Jechow, A., Kyba, C.C.M., Hölker, F., 2020. Mapping the brightness and color of urban to rural skyglow with all-sky photometry. *Journal of Quantitative Spectroscopy and Radiative Transfer* 250, 106988. <https://doi.org/10.1016/j.jqsrt.2020.106988>
- Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. B* 346, 445–455. <https://doi.org/10.1098/rstb.1994.0161>
- Kyba, C.C.M., Ruhtz, T., Fischer, J., Hölker, F., 2011. Cloud Coverage Acts as an Amplifier for Ecological Light Pollution in Urban Ecosystems. *PLoS ONE* 6, e17307. <https://doi.org/10.1371/journal.pone.0017307>
- Lacoeuilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., Kerbirou, C., 2014. The Influence of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. *PLoS ONE* 9, e103042. <https://doi.org/10.1371/journal.pone.0103042>
- Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbirou, C., Fonderflick, J., Besnard, A., 2019. Reducing light pollution improves connectivity for bats in urban landscapes. *Landscape Ecol* 34, 793–809. <https://doi.org/10.1007/s10980-019-00803-0>
- Luo, B., Xu, R., Li, Y., Zhou, W., Wang, W., Gao, H., Wang, Z., Deng, Y., Liu, Y., Feng, J., 2021. Artificial light reduces foraging opportunities in wild least horseshoe bats. *Environmental Pollution* 288, 117765. <https://doi.org/10.1016/j.envpol.2021.117765>
- Mariton, L., Kerbirou, 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. *Environmental Pollution* 305, 119267. <https://doi.org/10.1016/j.envpol.2022.119267>
- Mariton, L., Le Viol, I., Bas, Y., Kerbirou, C., accepted. Characterising diel activity patterns to design conservation measures: case study of European bat species. *Biological Conservation*.
- Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., Langton, S., 2015. Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Phil. Trans. R. Soc. B* 370, 20140124. <https://doi.org/10.1098/rstb.2014.0124>
- Pauwels, J., Le Viol, I., Azam, C., Valet, N., Julien, J.-F., Bas, Y., Lemarchand, C., Sánchez de Miguel, A., Kerbirou, C., 2019. Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landscape and Urban Planning* 183, 12–25. <https://doi.org/10.1016/j.landurbplan.2018.08.030>
- Racey, P.A., Speakman, J.R., 1987. The energy costs of pregnancy and lactation in heterothermic bats. *Symp. zool. Soc. Lond.* 107–125.
- Revilla-Martín, N., Budinski, I., Puig-Montserrat, X., Flaquer, C., López-Baucells, A., 2020. Monitoring cave-dwelling bats using remote passive acoustic detectors: a new approach for cave monitoring. *Bioacoustics* 1–16. <https://doi.org/10.1080/09524622.2020.1816492>

Bibliography

- Robinson, M.F., Stebbings, R.E., 1993. Food of the serotine bat, *Eptesicus serotinus* —is faecal analysis a valid qualitative and quantitative technique? *Journal of Zoology* 231, 239–248. <https://doi.org/10.1111/j.1469-7998.1993.tb01915.x>
- Rydell, J., 1992. Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology* 6, 744–750. <https://doi.org/10.2307/2389972>
- Salinas-Ramos, V.B., Ancillotto, L., Cistrone, L., Natasi, C., Bosso, L., Smeraldo, S., Sánchez-Cordero, V., Russo, D., 2021. Artificial illumination influences niche segregation in bats. *Environmental Pollution* 284, 117187. <https://doi.org/10.1016/j.envpol.2021.117187>
- Stone, E.L., Harris, S., Jones, G., 2015. Impacts of artificial lighting on bats: a review of challenges and solutions. *Mammalian Biology* 80, 213–219. <https://doi.org/10.1016/j.mambio.2015.02.004>
- Stone, E.L., Jones, G., Harris, S., 2009. Street Lighting Disturbs Commuting Bats. *Current Biology* 19, 1123–1127. <https://doi.org/10.1016/j.cub.2009.05.058>
- Tiede, J., Diepenbruck, M., Gadau, J., Wemheuer, B., Daniel, R., Scherber, C., 2020. Seasonal variation in the diet of the serotine bat (*Eptesicus serotinus*): A high-resolution analysis using DNA metabarcoding. *Basic and Applied Ecology* S1439179120300992. <https://doi.org/10.1016/j.baae.2020.09.004>
- UICN France, MNHN, SFEPM, ONCFS, 2017. La Liste rouge des espèces menacées en France – Chapitre Mammifères de France métropolitaine. Paris, France.
- van Grunsven, R.H.A., van Deijk, J.R., Donners, M., Berendse, F., Visser, M.E., Veenendaal, E.M., Spoelstra, K., 2020. Experimental light at night has a negative long-term impact on macro-moth populations. *Current Biology* 30, R694–R695. <https://doi.org/10.1016/j.cub.2020.04.083>
- Voigt, C.C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens, H.J.G.A., Mathews, F., Rydell, J., Spoelstra, K., Zagmajster, M., 2021. The Impact Of Light Pollution On Bats Varies According To Foraging Guild And Habitat Context. *BioScience* 71, 1103–1109. <https://doi.org/10.1093/biosci/biab087>
- Voigt, C.C., Scholl, J.M., Bauer, J., Teige, T., Yovel, Y., Kramer-Schadt, S., Gras, P., 2020. Movement responses of common noctule bats to the illuminated urban landscape. *Landscape Ecol* 35, 189–201. <https://doi.org/10.1007/s10980-019-00942-4>
- Ware, R.L., Garrod, B., Macdonald, H., Allaby, R.G., 2020. Guano morphology has the potential to inform conservation strategies in British bats. *PLoS ONE* 15, e0230865. <https://doi.org/10.1371/journal.pone.0230865>
- 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 Change Biol* 24, 5909–5918. <https://doi.org/10.1111/gcb.14462>

Chapter 3: Are technological developments in lighting threats to bats? (Context and Perspectives)

- Aubé, M., Simoneau, A., Wainscoat, R., Nelson, L., 2018. Modelling the effects of phosphor converted LED lighting to the night sky of the Haleakala Observatory, Hawaii. *Monthly Notices of the Royal Astronomical Society* 478, 1776–1783. <https://doi.org/10.1093/mnras/sty1143>
- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., Kerbiriou, C., 2018. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning* 175, 123–135. <https://doi.org/10.1016/j.landurbplan.2018.02.011>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., Kerbiriou, C., 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecol* 31, 2471–2483. <https://doi.org/10.1007/s10980-016-0417-3>
- Balbi, M., Petit, E.J., Croci, S., Nabucet, J., Georges, R., Madec, L., Ernoult, A., 2019. Title: Ecological relevance of least cost path analysis: An easy implementation method for landscape urban planning. *Journal of Environmental Management* 244, 61–68. <https://doi.org/10.1016/j.jenvman.2019.04.124>
- Barré, K., Kerbiriou, C., Ing, R.-K., Bas, Y., Azam, C., Le Viol, I., Spoelstra, K., 2021a. Bats seek refuge in cluttered environment when exposed to white and red lights at night. *Mov Ecol* 9, 3. <https://doi.org/10.1186/s40462-020-00238-2>
- Barré, K., Vernet, A., Azam, C., Le Viol, I., Dumont, A., Deana, T., Vincent, S., Challéat, S., Kerbiriou, C., 2021b. Landscape composition drives the impacts of artificial light at night on insectivorous bats. *Environmental Pollution* 292, 118394. <https://doi.org/10.1016/j.envpol.2021.118394>
- Bas, Y., Roemer, C., Julien, J.-F., 2020. Bat population trends [WWW Document]. Team-Chiro. URL <https://croemer3.wixsite.com/teamchiro/population-trends?lang=fr> (accessed 9.30.21).
- Bolliger, J., Haller, J., Wermelinger, B., Blum, S., Obrist, M.K., 2022. Contrasting impacts of street light shapes and LED color temperatures on nocturnal insects and bats. *Basic and Applied Ecology* S1439179122000615. <https://doi.org/10.1016/j.baae.2022.07.002>
- Bolliger, J., Hennen, T., Wermelinger, B., Blum, S., Haller, J., Obrist, M.K., 2020. Low impact of two LED colors on nocturnal insect abundance and bat activity in a peri-urban environment. *J Insect Conserv*. <https://doi.org/10.1007/s10841-020-00235-1>
- Briolat, E.S., Gaston, K.J., Bennie, J., Rosenfeld, E.J., Troscianko, J., 2021. Artificial nighttime lighting impacts visual ecology links between flowers, pollinators and predators. *Nat Commun* 12, 4163. <https://doi.org/10.1038/s41467-021-24394-0>
- Cushman, S., Lewis, J., Landguth, E., 2014. Why Did the Bear Cross the Road? Comparing the Performance of Multiple Resistance Surfaces and Connectivity Modeling Methods. *Diversity* 6, 844–854. <https://doi.org/10.3390/d6040844>
- Elvidge, C.D., Zhizhin, M., Ghosh, T., Hsu, F.-C., Taneja, J., 2021. Annual Time Series of Global VIIRS Nighttime Lights Derived from Monthly Averages: 2012 to 2019. *Remote Sensing* 13, 922. <https://doi.org/10.3390/rs13050922>
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecol Biogeography* 16, 265–280. <https://doi.org/10.1111/j.1466-8238.2007.00287.x>

Bibliography

- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J Appl Ecol* 50, 252–261. <https://doi.org/10.1111/1365-2664.12034>
- Froidevaux, J.S.P., Boughéy, K.L., Barlow, K.E., Jones, G., 2017. Factors driving population recovery of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the UK: implications for conservation. *Biodivers Conserv* 26, 1601–1621. <https://doi.org/10.1007/s10531-017-1320-1>
- Gaston, K.J., de Miguel, A.S., 2022. Environmental Impacts of Artificial Light at Night. *Annu. Rev. Environ. Resour.* 47, 8.1-8.26. <https://doi.org/10.1146/annurev-environ-112420-014438>
- Haddock, J.K., Threlfall, C.G., Law, B., Hochuli, D.F., 2019. Responses of insectivorous bats and nocturnal insects to local changes in street light technology: Insectivorous bats and street light technology. *Austral Ecology* 44, 1052–1064. <https://doi.org/10.1111/aec.12772>
- Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G., Sadler, J.P., 2015. The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Glob Change Biol* 21, 2467–2478. <https://doi.org/10.1111/gcb.12884>
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D., Hänel, A., Kappeler, P.M., Völker, S., Schwöpe, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C., Tockner, K., 2010. The Dark Side of Light: A Transdisciplinary Research Agenda for Light Pollution Policy. *E&S* 15, 13. <https://doi.org/10.5751/ES-03685-150413>
- Korpach, A.M., Garroway, C.J., Mills, A.M., von Zuben, V., Davy, C.M., Fraser, K.C., 2022. Urbanization and artificial light at night reduce the functional connectivity of migratory aerial habitat. *Ecography* e05581. <https://doi.org/10.1111/ecog.05581>
- Kyba, C.C.M., 2018. Is light pollution getting better or worse? *Nat Astron* 2, 267–269. <https://doi.org/10.1038/s41550-018-0402-7>
- 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>
- Lacoeuilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., Kerbirou, C., 2014. The Influence of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. *PLoS ONE* 9, e103042. <https://doi.org/10.1371/journal.pone.0103042>
- Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbirou, C., Fonderflick, J., Besnard, A., 2019. Reducing light pollution improves connectivity for bats in urban landscapes. *Landscape Ecol* 34, 793–809. <https://doi.org/10.1007/s10980-019-00803-0>
- Lewanzik, D., Straka, T.M., Lorenz, J., Marggraf, L., Voigt-Heucke, S.L., Schumann, A., Brandt, M., Voigt, C.C., 2021. Evaluating the potential of urban areas for bat conservation with citizen science data. *Environmental Pollution* 118785. <https://doi.org/10.1016/j.envpol.2021.118785>
- Lewanzik, D., Voigt, C.C., 2017. Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *J Appl Ecol* 54, 264–271. <https://doi.org/10.1111/1365-2664.12758>
- Lockett, M.T., Jones, T.M., Elgar, M.A., Gaston, K.J., Visser, M.E., Hopkins, G.R., 2021. Urban street lighting differentially affects community attributes of airborne and ground-dwelling invertebrate assemblages. *J Appl Ecol* 1365-2664.13969. <https://doi.org/10.1111/1365-2664.13969>
- Mariton, L., Kerbirou, 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. *Environmental Pollution* 305, 119267.
<https://doi.org/10.1016/j.envpol.2022.119267>
- McNaughton, E.J., Beggs, J.R., Gaston, K.J., Jones, D.N., Stanley, M.C., 2021. Retrofitting streetlights with LEDs has limited impacts on urban wildlife. *Biological Conservation* 254, 108944. <https://doi.org/10.1016/j.biocon.2020.108944>
- Miller, C.R., Barton, B.T., Zhu, L., Radeloff, V.C., Oliver, K.M., Harmon, J.P., Ives, A.R., 2017. Combined effects of night warming and light pollution on predator–prey interactions. *Proc. R. Soc. B.* 284, 20171195. <https://doi.org/10.1098/rspb.2017.1195>
- Mimet, A., Kerbiriou, C., Simon, L., Julien, J.-F., Raymond, R., 2020. Contribution of private gardens to habitat availability, connectivity and conservation of the common pipistrelle in Paris. *Landscape and Urban Planning* 193, 103671.
<https://doi.org/10.1016/j.landurbplan.2019.103671>
- Pauwels, J., Le Viol, I., Azam, C., Valet, N., Julien, J.-F., Bas, Y., Lemarchand, C., Sánchez de Miguel, A., Kerbiriou, C., 2019. Accounting for artificial light impact on bat activity for a biodiversity-friendly urban planning. *Landscape and Urban Planning* 183, 12–25. <https://doi.org/10.1016/j.landurbplan.2018.08.030>
- Pauwels, J., Le Viol, I., Mariton, L., Laforge, A., Bas, Y., Coulon, A., Valet, N., Besnard, A., Fonderflick, J., Kerbiriou, C., in prep. Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas.
- Pawson, S.M., Bader, M.K.-F., 2014. LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications* 24, 1561–1568.
<https://doi.org/10.1890/14-0468.1>
- Pinaud, D., Claireau, F., Leuchtmann, M., Kerbiriou, C., 2018. Modelling landscape connectivity for greater horseshoe bat using an empirical quantification of resistance. *J Appl Ecol* 55, 2600–2611. <https://doi.org/10.1111/1365-2664.13228>
- Rodríguez, A., Rodríguez, B., Negro, J.J., 2015. GPS tracking for mapping seabird mortality induced by light pollution. *Sci Rep* 5, 10670. <https://doi.org/10.1038/srep10670>
- 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>
- Rowse, E.G., Harris, S., Jones, G., 2016. The Switch from Low-Pressure Sodium to Light Emitting Diodes Does Not Affect Bat Activity at Street Lights. *PLoS ONE* 11, e0150884. <https://doi.org/10.1371/journal.pone.0150884>
- Russo, D., Ancillotto, L., 2015. Sensitivity of bats to urbanization: a review. *Mammalian Biology* 80, 205–212. <https://doi.org/10.1016/j.mambio.2014.10.003>
- 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. *Environmental Pollution* 252, 1671–1677.
<https://doi.org/10.1016/j.envpol.2019.06.105>
- Sánchez de Miguel, A., Bennie, J., Rosenfeld, E., Dzurjak, S., Gaston, K.J., 2022. Environmental risks from artificial nighttime lighting widespread and increasing across Europe. *Sci. Adv.* 8, eabl6891. <https://doi.org/10.1126/sciadv.abl6891>
- Sánchez de Miguel, A., Zamorano, J., Aubé, M., Bennie, J., Gallego, J., Ocaña, F., Pettit, D.R., Stefanov, W.L., Gaston, K.J., 2021. Colour remote sensing of the impact of artificial light at night (II): Calibration of DSLR-based images from the International Space Station. *Remote Sensing of Environment* 112611.
<https://doi.org/10.1016/j.rse.2021.112611>
- Seewagen, C.L., Adams, A.M., 2021. Turning to the dark side: LED light at night alters the activity and species composition of a foraging bat assemblage in the northeastern United States. *Ecol Evol* ece3.7466. <https://doi.org/10.1002/ece3.7466>

Bibliography

- Somers-Yeates, R., Hodgson, D., McGregor, P.K., Spalding, A., ffrench-Constant, R.H., 2013. Shedding light on moths: shorter wavelengths attract noctuids more than geometrids. *Biol. Lett.* 9, 20130376. <https://doi.org/10.1098/rsbl.2013.0376>
- Spoelstra, K., Ramakers, J.J.C., van Dis, N.E., Visser, M.E., 2018. No effect of artificial light of different colors on commuting Daubenton's bats (*Myotis daubentonii*) in a choice experiment. *J. Exp. Zool.* 329, 506–510. <https://doi.org/10.1002/jez.2178>
- 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.* 284, 20170075. <https://doi.org/10.1098/rspb.2017.0075>
- Stone, E.L., Jones, G., Harris, S., 2012. Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Glob Change Biol* 18, 2458–2465. <https://doi.org/10.1111/j.1365-2486.2012.02705.x>
- Straka, T.M., Greif, S., Schultz, S., Goerlitz, H.R., Voigt, C.C., 2020. The effect of cave illumination on bats. *Global Ecology and Conservation* 21, e00808. <https://doi.org/10.1016/j.gecco.2019.e00808>
- Zissis, G., Bertoldi, P., Serrenho, T., 2021. Update on the status of LED-lighting world market since 2018 (JRC Technical Report No. EUR 30500 EN). Publications Office of the European Union, Luxembourg.

General discussion

- Agence de la transition écologique — ADEME Expertises, n.d. Éclairage public : un gisement d'économies d'énergie [WWW Document]. Agence de la transition écologique. URL <https://expertises.ademe.fr/collectivites-secteur-public/patrimoine-communes-comment-passer-a-laction/eclairage-public-gisement-deconomies-denergie> (accessed 12.10.22).
- ANPCEN, 2021. 364 communes françaises dans 76 départements labellisées « Villes et Villages Étoilés » et 4 territoires distingués par l'ANPCEN !
- 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*). *Biological Conservation* 93, 55–60. [https://doi.org/10.1016/S0006-3207\(99\)00112-3](https://doi.org/10.1016/S0006-3207(99)00112-3)
- Arrêté du 27 décembre 2018 relatif à la prévention, à la réduction et à la limitation des nuisances lumineuses, 2018. , Journal officiel de la République française.
- Arthur, L., Lemaire, M., 2015. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope ; Museum national d'Histoire Naturelle, Mèze; Paris.
- Article L4251-3, n.d. , Code général des collectivités territoriales.
- Aschoff, J., 1989. Temporal orientation: circadian clocks in animals and humans. *Animal Behaviour* 37, 881–896. [https://doi.org/10.1016/0003-3472\(89\)90132-2](https://doi.org/10.1016/0003-3472(89)90132-2)
- 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 Change Biol* 21, 4333–4341. <https://doi.org/10.1111/gcb.13036>
- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., Kerbiriou, C., 2018. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning* 175, 123–135. <https://doi.org/10.1016/j.landurbplan.2018.02.011>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., Kerbiriou, C., 2016. Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecol* 31, 2471–2483. <https://doi.org/10.1007/s10980-016-0417-3>
- Barré, K., Froidevaux, J.S.P., Leroux, C., Mariton, L., Fritze, M., Kerbiriou, C., Le Viol, I., Bas, Y., Roemer, C., 2022. Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: A call for action. *Conservat Sci and Prac* 4, e12805. <https://doi.org/10.1111/csp2.12805>
- Barré, K., Spoelstra, K., Bas, Y., Challéat, S., Ing, R.-K., Azam, C., Zissis, G., Lapostolle, D., Kerbiriou, C., Le Viol, I., 2020. Artificial light may change flight patterns of bats near bridges along urban waterways. *Anim Conserv acv*.12635. <https://doi.org/10.1111/acv.12635>
- Barré, K., Vernet, A., Azam, C., Le Viol, I., Dumont, A., Deana, T., Vincent, S., Challéat, S., Kerbiriou, C., 2021. Landscape composition drives the impacts of artificial light at night on insectivorous bats. *Environmental Pollution* 292, 118394. <https://doi.org/10.1016/j.envpol.2021.118394>
- Battisti, C., 2003. Habitat fragmentation, fauna and ecological network planning: Toward a theoretical conceptual framework. *Italian Journal of Zoology* 70, 241–247. <https://doi.org/10.1080/11250000309356524>
- Beaudet, C., Tardieu, L., David, M., 2022. Are citizens willing to accept changes in public lighting for biodiversity conservation? *Ecological Economics* 200, 107527. <https://doi.org/10.1016/j.ecolecon.2022.107527>

Bibliography

- Bennie, J., Davies, T.W., Cruse, D., Inger, R., Gaston, K.J., 2018. Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *J Appl Ecol* 55, 2698–2706. <https://doi.org/10.1111/1365-2664.13240>
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)
- Borgström, S.T., Elmqvist, T., Angelstam, P., Alfsen-Norodom, C., 2006. Scale Mismatches in Management of Urban Landscapes. *E&S* 11, art16. <https://doi.org/10.5751/ES-01819-110216>
- Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., Pocock, M.J.O., 2021. Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* 7, eabi8322. <https://doi.org/10.1126/sciadv.abi8322>
- Busson, S., Carat, D., 2020. Intégrer les enjeux de biodiversité nocturne dans la planification et les outils opérationnels.
- Chalfin, A., Hansen, B., Lerner, J., Parker, L., 2022. Reducing Crime Through Environmental Design: Evidence from a Randomized Experiment of Street Lighting in New York City. *J Quant Criminol* 38, 127–157. <https://doi.org/10.1007/s10940-020-09490-6>
- Challéat, S., Barré, K., Laforge, A., Lapostolle, D., Franchomme, M., Sirami, C., Le Viol, I., Milian, J., Kerbirou, C., 2021. Grasping darkness: the dark ecological network as a social-ecological framework to limit the impacts of light pollution on biodiversity. *E&S* 26, art15. <https://doi.org/10.5751/ES-12156-260115>
- Chen, Y., Tan, J., Liu, Y., Dong, G.-H., Yang, B.-Y., Li, N., Wang, L., Chen, G., Li, S., Guo, Y., 2022. Long-term exposure to outdoor light at night and mild cognitive impairment: A nationwide study in Chinese veterans. *Science of The Total Environment* 847, 157441. <https://doi.org/10.1016/j.scitotenv.2022.157441>
- Cisneros, L.M., Fagan, M.E., Willig, M.R., 2015. Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity Distrib.* 21, 523–533. <https://doi.org/10.1111/ddi.12277>
- Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for bat conservation: Part-night lighting and bats. *Anim Conserv* 18, 512–516. <https://doi.org/10.1111/acv.12200>
- de Jong, M., Ouyang, J.Q., Da Silva, A., van Grunsven, R.H.A., Kempnaers, B., Visser, M.E., Spoelstra, K., 2015. Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species. *Phil. Trans. R. Soc. B* 370, 20140128. <https://doi.org/10.1098/rstb.2014.0128>
- Downs, N.C., Beaton, V., Guest, J., Polanski, J., Robinson, S.L., Racey, P.A., 2003. The effects of illuminating the roost entrance on the emergence behaviour of *Pipistrellus pygmaeus*. *Biological Conservation* 111, 247–252. [https://doi.org/10.1016/S0006-3207\(02\)00298-7](https://doi.org/10.1016/S0006-3207(02)00298-7)
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- Eisenbeis, G., 2006. Artificial night lighting and insects: attraction of insects to streetlamps in a rural setting in Germany, in: *Ecological Consequences of Artificial Night Lighting*. Washington DC, pp. 281–304.
- Elvidge, C.D., Zhizhin, M., Ghosh, T., Hsu, F.-C., Taneja, J., 2021. Annual Time Series of Global VIIRS Nighttime Lights Derived from Monthly Averages: 2012 to 2019. *Remote Sensing* 13, 922. <https://doi.org/10.3390/rs13050922>

Bibliography

- 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., 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>
- Fédération des Parcs naturels régionaux, n.d. Missions [WWW Document]. Fédération des Parcs naturels régionaux. URL <https://www.parcs-naturels-regionaux.fr/les-parcs/missions> (accessed 12.18.22).
- Franchomme, M., Hinnewinkel, C., Challéat, S., 2019. La trame noire, un indicateur de la place de la nature dans l'aménagement du territoire: Pratiques et motivations des communes de la Métropole européenne de Lille. *bagf* 96, 161–180.
<https://doi.org/10.4000/bagf.4764>
- Froidevaux, J.S.P., Boughey, K.L., Barlow, K.E., Jones, G., 2017. Factors driving population recovery of the greater horseshoe bat (*Rhinolophus ferrumequinum*) in the UK: implications for conservation. *Biodivers Conserv* 26, 1601–1621.
<https://doi.org/10.1007/s10531-017-1320-1>
- Gardella, O., 2022. Les pratiques communales en matière d'éclairage public au sein des Parcs Naturels Régionaux Français (Mémoire de Master I). Université Paris Cité, Paris.
- Gaston, K.J., Bennie, J., 2014. Demographic effects of artificial nighttime lighting on animal populations. *Environ. Rev.* 22, 323–330. <https://doi.org/10.1139/er-2014-0005>
- Gaston, K.J., Davies, T.W., Bennie, J., Hopkins, J., 2012. REVIEW: Reducing the ecological consequences of night-time light pollution: options and developments. *J Appl Ecol* 49, 1256–1266. <https://doi.org/10.1111/j.1365-2664.2012.02212.x>
- Haddock, J.K., Threlfall, C.G., Law, B., Hochuli, D.F., 2019. Light pollution at the urban forest edge negatively impacts insectivorous bats. *Biological Conservation* 236, 17–28. <https://doi.org/10.1016/j.biocon.2019.05.016>
- Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G., Sadler, J.P., 2015. The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. *Glob Change Biol* 21, 2467–2478. <https://doi.org/10.1111/gcb.12884>
- Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats. *Environmental Pollution* 307, 119552.
<https://doi.org/10.1016/j.envpol.2022.119552>
- Hunter, S.B., zu Ermgassen, S.O.S.E., Downey, H., Griffiths, R.A., Howe, C., 2021. Evidence shortfalls in the recommendations and guidance underpinning ecological mitigation for infrastructure developments. *Ecological Solutions and Evidence* 2. <https://doi.org/10.1002/2688-8319.12089>
- International Dark-Sky Association, n.d. International Dark Sky Reserves. International Dark-Sky Association. URL <https://www.darksky.org/our-work/conservation/idsp/reserves/> (accessed 12.11.22).
- Jeliazkov, A., Bas, Y., Kerbiriou, C., Julien, J.-F., Penone, C., Le Viol, I., 2016. Large-scale semi-automated acoustic monitoring allows to detect temporal decline of bush-crickets. *Global Ecology and Conservation* 6, 208–218.
<https://doi.org/10.1016/j.gecco.2016.02.008>
- Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Phil. Trans. R. Soc. Lond. B* 346, 445–455.
<https://doi.org/10.1098/rstb.1994.0161>

Bibliography

- Kerbiriou, C., Barré, K., Mariton, L., Pauwels, J., Zissis, G., Robert, A., Le Viol, I., 2020. Switching LPS to LED Streetlight May Dramatically Reduce Activity and Foraging of Bats. *Diversity* 12, 165. <https://doi.org/10.3390/d12040165>
- 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>
- Lacoeuilhe, A., Machon, N., Julien, J.-F., Le Bocq, A., Kerbiriou, C., 2014. The Influence of Low Intensities of Light Pollution on Bat Communities in a Semi-Natural Context. *PLoS ONE* 9, e103042. <https://doi.org/10.1371/journal.pone.0103042>
- Laforge, A., Barbaro, L., Bas, Y., Calatayud, F., Ladet, S., Sirami, C., Archaux, F., 2022. Road density and forest fragmentation shape bat communities in temperate mosaic landscapes. *Landscape and Urban Planning* 221, 104353. <https://doi.org/10.1016/j.landurbplan.2022.104353>
- Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbiriou, C., Fonderflick, J., Besnard, A., 2019. Reducing light pollution improves connectivity for bats in urban landscapes. *Landscape Ecol* 34, 793–809. <https://doi.org/10.1007/s10980-019-00803-0>
- Lai, K.Y., Sarkar, C., Ni, M.Y., Cheung, L.W.T., Gallacher, J., Webster, C., 2021. Exposure to light at night (LAN) and risk of breast cancer: A systematic review and meta-analysis. *Science of The Total Environment* 762, 143159. <https://doi.org/10.1016/j.scitotenv.2020.143159>
- Lai, K.Y., Sarkar, C., Ni, M.Y., Gallacher, J., Webster, C., 2020. Exposure to light at night (LAN) and risk of obesity: A systematic review and meta-analysis of observational studies. *Environmental Research* 187, 109637. <https://doi.org/10.1016/j.envres.2020.109637>
- Lapostolle, D., Challéat, S., 2019. Lutter contre la pollution lumineuse: Trois processus de valorisation de l'obscurité dans les territoires français. *vertigo*. <https://doi.org/10.4000/vertigo.26057>
- Le Tallec, T., Théry, M., Perret, M., 2015. Effects of light pollution on seasonal estrus and daily rhythms in a nocturnal primate. *JMAMMAL* 96, 438–445. <https://doi.org/10.1093/jmammal/gyv047>
- Lewanzik, D., Straka, T.M., Lorenz, J., Marggraf, L., Voigt-Heucke, S.L., Schumann, A., Brandt, M., Voigt, C.C., 2021. Evaluating the potential of urban areas for bat conservation with citizen science data. *Environmental Pollution* 118785. <https://doi.org/10.1016/j.envpol.2021.118785>
- Limesurvey GmbH, n.d. LimeSurvey: An Open Source survey tool.
- LOI n° 2009-967 du 3 août 2009 de programmation relative à la mise en œuvre du Grenelle de l'environnement (1), 2009. , Journal officiel de la République française.
- Luo, B., Xu, R., Li, Y., Zhou, W., Wang, W., Gao, H., Wang, Z., Deng, Y., Liu, Y., Feng, J., 2021. Artificial light reduces foraging opportunities in wild least horseshoe bats. *Environmental Pollution* 288, 117765. <https://doi.org/10.1016/j.envpol.2021.117765>
- Lyytimäki, J., Rinne, J., 2013. Voices for the darkness: online survey on public perceptions on light pollution as an environmental problem. *Journal of Integrative Environmental Sciences* 10, 127–139. <https://doi.org/10.1080/1943815X.2013.824487>
- 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. *Environmental Pollution* 305, 119267. <https://doi.org/10.1016/j.envpol.2022.119267>

Bibliography

- Mariton, L., Le Viol, I., Bas, Y., Kerbiriou, C., accepted. Characterising diel activity patterns to design conservation measures: case study of European bat species. *Biological Conservation*.
- Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., Langton, S., 2015. Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Phil. Trans. R. Soc. B* 370, 20140124. <https://doi.org/10.1098/rstb.2014.0124>
- McAney, C.M., Fairley, J.S., 1988. Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at summer roosts. *Journal of Zoology* 216, 325–338. <https://doi.org/10.1111/j.1469-7998.1988.tb02433.x>
- Müller, B., Glösmann, M., Peichl, L., Knop, G.C., Hagemann, C., Ammermüller, J., 2009. Bat Eyes Have Ultraviolet-Sensitive Cone Photoreceptors. *PLoS ONE* 4, e6390. <https://doi.org/10.1371/journal.pone.0006390>
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>
- Orbach, D.N., Fenton, B., 2010. Vision Impairs the Abilities of Bats to Avoid Colliding with Stationary Obstacles. *PLoS ONE* 5, e13912. <https://doi.org/10.1371/journal.pone.0013912>
- Owens, A.C.S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E.K., Seymoure, B.M., 2019. Light pollution is a driver of insect declines. *Biological Conservation* 241, 108259. <https://doi.org/10.1016/j.biocon.2019.108259>
- Painter, K., 1996. The influence of street lighting improvements on crime, fear and pedestrian street use, after dark. *Landscape and Urban Planning* 35, 193–201. [https://doi.org/10.1016/0169-2046\(96\)00311-8](https://doi.org/10.1016/0169-2046(96)00311-8)
- Pauwels, J., Le Viol, I., Mariton, L., Laforge, A., Bas, Y., Coulon, A., Valet, N., Besnard, A., Fonderflick, J., Kerbiriou, C., in prep. Flying through the city: new lighting technologies alter landscape connectivity for bats in urban areas.
- Polak, T., Korine, C., Yair, S., Holderied, M.W., 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert: Light pollution in deserts and bat foraging. *Journal of Zoology*. <https://doi.org/10.1111/j.1469-7998.2011.00808.x>
- Roche, N., Langton, S., Aughney, T., Russ, J.M., Marnell, F., Lynn, D., Catto, C., 2011. A car-based monitoring method reveals new information on bat populations and distributions in Ireland: Car-based bat monitoring in Ireland. *Anim Conserv* 14, 642–651. <https://doi.org/10.1111/j.1469-1795.2011.00470.x>
- Rydell, J., 1992. Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology* 6, 744–750. <https://doi.org/10.2307/2389972>
- Rydell, J., Entwistle, A.C., 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., Natasi, C., Bosso, L., Smeraldo, S., Sánchez-Cordero, V., Russo, D., 2021. Artificial illumination influences niche segregation in bats. *Environmental Pollution* 284, 117187. <https://doi.org/10.1016/j.envpol.2021.117187>
- Sánchez de Miguel, A., Bennie, J., Rosenfeld, E., Dzurjak, S., Gaston, K.J., 2022. Environmental risks from artificial nighttime lighting widespread and increasing across Europe. *Sci. Adv.* 8, eabl6891. <https://doi.org/10.1126/sciadv.abl6891>

Bibliography

- Senzaki, M., Barber, J.R., Phillips, J.N., Carter, N.H., Cooper, C.B., Ditmer, M.A., Fristrup, K.M., McClure, C.J.W., Mennitt, D.J., Tyrrell, L.P., Vukomanovic, J., Wilson, A.A., Francis, C.D., 2020. Sensory pollutants alter bird phenology and fitness across a continent. *Nature*. <https://doi.org/10.1038/s41586-020-2903-7>
- Silver, D.A., Hickey, G.M., 2020. Managing light pollution through dark sky areas: learning from the world's first dark sky preserve. *Journal of Environmental Planning and Management* 63, 2627–2645. <https://doi.org/10.1080/09640568.2020.1742675>
- Sordello, R., Busson, S., Cornuau, J.H., Deverchère, P., Faure, B., Guetté, A., Hölker, F., Kerbirou, C., Lengagne, T., Le Viol, I., Longcore, T., Moeschler, P., Ranzoni, J., Ray, N., Reyjol, Y., Roulet, Y., Schroer, S., Secondi, J., Valet, N., Vanpeene, S., Vauclair, S., 2022. A plea for a worldwide development of dark infrastructure for biodiversity – Practical examples and ways to go forward. *Landscape and Urban Planning* 219, 104332. <https://doi.org/10.1016/j.landurbplan.2021.104332>
- 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* 284, 20170075. <https://doi.org/10.1098/rspb.2017.0075>
- Steinbach, R., Perkins, C., Tompson, L., Johnson, S., Armstrong, B., Green, J., Grundy, C., Wilkinson, P., Edwards, P., 2015. The effect of reduced street lighting on road casualties and crime in England and Wales: controlled interrupted time series analysis. *J Epidemiol Community Health* 69, 1118–1124. <https://doi.org/10.1136/jech-2015-206012>
- Stone, E.L., Harris, S., Jones, G., 2015. Impacts of artificial lighting on bats: a review of challenges and solutions. *Mammalian Biology* 80, 213–219. <https://doi.org/10.1016/j.mambio.2015.02.004>
- Straka, T.M., Wolf, M., Gras, P., Buchholz, S., Voigt, C.C., 2019. Tree Cover Mediates the Effect of Artificial Light on Urban Bats. *Front. Ecol. Evol.* 7, 91. <https://doi.org/10.3389/fevo.2019.00091>
- Sutherland, W.J., Taylor, N.G., MacFarlane, D., Amano, T., Christie, A.P., Dicks, L.V., Lemasson, A.J., Littlewood, N.A., Martin, P.A., Ockendon, N., Petrovan, S.O., Robertson, R.J., Rocha, R., Shackelford, G.E., Smith, R.K., Tyler, E.H.M., Wordley, C.F.R., 2019. Building a tool to overcome barriers in research-implementation spaces: The Conservation Evidence database. *Biological Conservation* 238, 108199. <https://doi.org/10.1016/j.biocon.2019.108199>
- Tancredi, S., Urbano, T., Vinceti, M., Filippini, T., 2022. Artificial light at night and risk of mental disorders: A systematic review. *Science of The Total Environment* 833, 155185. <https://doi.org/10.1016/j.scitotenv.2022.155185>
- Tompson, L., Steinbach, R., Johnson, S.D., Teh, C.S., Perkins, C., Edwards, P., Armstrong, B., 2022. Absence of Street Lighting May Prevent Vehicle Crime, but Spatial and Temporal Displacement Remains a Concern. *J Quant Criminol*. <https://doi.org/10.1007/s10940-022-09539-8>
- van Klink, R., August, T., Bas, Y., Bodesheim, P., Bonn, A., Fossøy, F., Høye, T.T., Jongejans, E., Menz, M.H.M., Miraldo, A., Roslin, T., Roy, H.E., Ruczyński, I., Schigel, D., Schäffler, L., Sheard, J.K., Svenningsen, C., Tschann, G.F., Wäldchen, J., Zizka, V.M.A., Åström, J., Bowler, D.E., 2022. Emerging technologies revolutionise insect ecology and monitoring. *Trends in Ecology & Evolution* S0169534722001343. <https://doi.org/10.1016/j.tree.2022.06.001>
- Voigt, C.C., Dekker, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Lewanzik, D., Limpens, H.J.G.A., Mathews, F., Rydell, J., Spoelstra, K., Zagamajster, M., 2021. The

Bibliography

- Impact Of Light Pollution On Bats Varies According To Foraging Guild And Habitat Context. *BioScience* 71, 1103–1109. <https://doi.org/10.1093/biosci/biab087>
- Welsh, B.C., Farrington, D.P., 2008. Effects of Improved Street Lighting on Crime. *Campbell Systematic Reviews* 4, 1–51. <https://doi.org/10.4073/csr.2008.13>
- 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 Change Biol* 24, 5909–5918. <https://doi.org/10.1111/gcb.14462>
- Zissis, G., Bertoldi, P., Serrenho, T., 2021. Update on the status of LED-lighting world market since 2018 (JRC Technical Report No. EUR 30500 EN). Publications Office of the European Union, Luxembourg.

Appendices

Appendix I: Online appendices of Mariton et al. (*accepted*)

Appendix A: Overview of scientific literature on bat diel activity patterns

To assess previous knowledge on bat diel activity patterns, we conducted a non-exhaustive review on scientific literature. In Google Scholar, for each species studied, we performed the following research: ("*activity pattern*" OR "*pattern of activity*" OR "*activity rhythm*" OR "*rhythm of activity*") AND "*Species latin name*" AND "sunset". "Sunset" was chosen as an additional filter because of its almost systematic use in papers dealing with bat diel activity patterns. We acknowledge that by only using English sources, our database does not reflect all published studies, however, we assume that it is a representative sample.

For the Great *Myotis* (group composed *Myotis myotis* and *Myotis blythii*) we performed separate researches on *M. myotis* and *M. blythii* (for the latter species, we also performed researches on *Myotis oxygnathus* as this Latin name is used in some studies). *Pipistrellus pygmaeus* was first described as a distinct species from *Pipistrellus pipistrellus* in 2003 (Jones and Froidevaux, 2020). Thus, studies published before 2003 and conducted in areas where both species can be found were attributed to (1) *P. pipistrellus* if the authors focused on a "45 kHz phonic type", to (2) *P. pygmaeus* if the authors focused on a "55 kHz phonic type" and to (3) the *P. pipistrellus/pygmaeus* complex if the authors gave no information on the phonic type studied.

We only kept studies that were conducted in Europe and that provided information on the diel activity patterns of given species (i.e. we discarded papers in which the diel activity patterns of all bat species combined were studied). We discarded studies on diel activity patterns inside hibernacula, swarming or nursery roosts. For each study kept, we specified the method used to give information on activity patterns. We considered that a study focused on the local scale when information on diel activity patterns was provided by monitoring a small number of individuals and/or by monitoring a small number of sites (less than 25). We specified whether the information on diel activity patterns provided by each study was related to the diel activity patterns at roost or at foraging/commuting sites.

We found 44 studies, 34 (77 %) only provided information on the diel activity pattern of a single species studied in this paper, nine (20 %) provided information on the diel activity pattern of two to four species and only one provided information on the activity pattern of five species or more. *P. pipistrellus* and *P. pygmaeus* were well represented (11 studies between the two of them, 25 %), followed by *Myotis daubentonii*, *Rhinolophus hipposideros* and *Nyctalus noctula* (eight, six and five studies respectively). The other species were less studied: six were in four studies, one in three studies, one in two studies and six in one study. We did not find any study (conducted in Europe) on the diel activity pattern of *Pipistrellus kuhlii*.

Different methods were regularly used simultaneously to provide information on bat diel activity patterns. Visual observations were used in 18 studies (41 %), acoustic monitoring in 17 studies (39 %), radiotracking in 14 studies (32%), other methods used were, for instance, infrared devices, cameras traps or GPS. Ten, 19 and 15 studies (23 %, 43 % and 34%) provided information on diel activity patterns at foraging/commuting sites, at roosts and at both roost and foraging/commuting sites respectively. There was hence a bias toward roost monitoring, with many studies focusing on the time of emergence. Almost all studies were conducted at local scales (41 studies, 93 %) with only three studies at the regional scale or more. The studies were unevenly distributed across Europe. For instance, 19 studies were conducted in the United-Kingdom (43 %) and six in Germany (14 %) while only one was conducted in France.

Table A.1: Overview of the scientific literature on the diel activity patterns of the 20 species studied in this paper. Species are named with their species codes (correspondence between codes and full Latin and English names in Table F). “Myossp” means *Myotis spp.* “Yes” in “Roost” means that the study provided information on diel activity patterns at roosts, “Yes” in “For. site” means that the study provided information on diel activity patterns at foraging/commuting sites.

Citation	Journal	Species	Country	Roost	For. site	Local	Method
(Ancillotto et al., 2018)	Behavioural Processes	Hypsav	Italy	Yes	No	Yes	Radiotracking
(Bartonička et al., 2008)	Annales Zoologici Fennici	Pippyg	Czech Republic	Yes	Yes	Yes	Radiotracking
(Bartonička and Řehák, 2004)	Mammalia	Pippyg	Czech Republic	No	Yes	Yes	Acoustic
(Boldogh et al., 2007)	Acta Chiropterologica	Myobly, Myoema, Rhifer	Hungary	Yes	No	Yes	Visual observations
(Bullock et al., 1987)	Journal of Zoology	Pippip/pyg	UK	Yes	No	Yes	Visual observations
(Catto et al., 1995)	Journal of Zoology	Eptser	UK	Yes	No	Yes	Infra-red/camera traps/video
(Ciechanowski et al., 2009)	Mammalia	Pipnat	Poland	No	Yes	Yes	Acoustic
(Day et al., 2015)	Animal Conservation	Rhifer	UK	No	Yes	No	Acoustic
(DeCoursey and DeCoursey, 1964)	The Biological Bulletin	Myomyo	Germany	Yes	No	Yes	Visual observations
(Dietz and Kalko, 2007)	Canadian Journal of Zoology	Myodau	Germany	Yes	Yes	Yes	Radiotracking
(Downs et al., 2016)	Acta Chiropterologica	Rhihip	UK	Yes	Yes	Yes	Radiotracking
(Duvergé et al., 2000)	Ecography	Rhifer, Rhihip	UK	Yes	No	Yes	Radiotracking + visual observations
(Encarnação et al., 2006)	Folia Zoologica - Praha	Myodau	Germany	Yes	Yes	Yes	Radiotracking + visual observations
(Entwistle et al., 1996)	Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences	Pleaur	UK	Yes	Yes	Yes	Radiotracking
(García-Ruiz et al., 2017)	Acta Chiropterologica	Minsch, Myobly/myo	Spain	Yes	No	Yes	Acoustic + infra-red/camera traps/video
(Gelhaus and Zahn, 2010)	Vespertilio	Pipnat	Germany	Yes	No	Yes	Visual observations

Citation	Journal	Species	Country	Roost	For. site	Local	Method
(Goodenough et al., 2015)	Wildlife Biology	Myonat, Nycnoc, Pippip, Pippyg	UK	No	Yes	Yes	Acoustic
(Guixé et al., 2016)	Barbastella	Rhihip	Spain	Yes	Yes	Yes	Infra-red/camera traps/video
(Hooker et al., 2022)	Environmental Pollution	Myospp	UK	No	Yes	Yes	Acoustic
(Jenkins et al., 1998)	Animal Behaviour	Pippyg	UK	Yes	No	Yes	Visual observations
(Kapfer and Aron, 2007)	Lutra	Myodau, Pipnat, Pippip	Belgium	No	Yes	Yes	Acoustic
(Lino et al., 2015)	Galemys, Spanish Journal of Mammalogy	Rhihip	Portugal	Yes	No	Yes	Infra-red/camera traps/video
(Maier, 1992)	Journal of Zoology	Pippip/pyg	UK	Yes	No	Yes	Visual observations
(Mariton et al., 2022)	Environmental Pollution	Eptser	France	No	Yes	No	Acoustic
(Marques et al., 2004)	Acta Chiropterologica	Tadten	Portugal	Yes	Yes	Yes	Radiotracking
(McAney and Fairley, 1988)	Journal of Zoology	Rhihip	Ireland	Yes	No	Yes	Acoustic + visual observations
(Newson et al., 2015)	Biological Conservation	Barbar, Eptser, Pipnat, Pippip, Pippyg, Pleaur, Myodau, Myomys, Myonat, Nyclei, Nycnoc	UK	No	Yes	No	Acoustic
(Rachwald, 1992)	Acta Theriologica	Nycnoc	Poland	No	Yes	Yes	Acoustic
(Razgour et al., 2011)	Biological Conservation	Pleaus	UK	Yes	Yes	Yes	Radiotracking
(Robinson and Stebbings, 1997)	Myotis	Eptser	UK	Yes	Yes	Yes	Radiotracking + visual observations
(Roeleke et al., 2016)	Scientific Reports	Nycnoc	Germany	Yes	Yes	Yes	GPS tracking

Citation	Journal	Species	Country	Roost	For. site	Local	Method
(Ruczyński et al., 2017)	Mammal Research	Nyclei, Nycnoc	Poland	Yes	Yes	Yes	Radiotracking + visual observations
(Rudolph et al., 2009)	Acta Chiropterologica	Myomyo	Germany	Yes	Yes	Yes	Radiotracking
(Russo et al., 2007)	Acta Oecologica	Barbar	Italy	Yes	No	Yes	Infra-red/camera traps/video
(Ružinská et al., 2022)	Scientific Reports	Myodau	Slovakia	Yes	No	Yes	Passive integrated transponders
(Rydell et al., 1996)	Oikos	Myodau, Pippyg, Pleaur	UK	Yes	Yes	Yes	Acoustic + radiotracking + visual observations
(Shiel and Fairley, 1999)	Journal of Zoology	Nyclei	Ireland	Yes	No	Yes	Acoustic + visual
(Shiel et al., 1999)	Journal of Zoology	Nyclei	Ireland	Yes	Yes	Yes	Radiotracking
(Stone et al., 2009)	Current Biology	Rhihip	UK	No	Yes	Yes	Acoustic + visual observations
(Swift, 1980)	Journal of Zoology	Pippip/pyg	UK	Yes	No	Yes	Visual observations
(Swift, 1997)	Journal of Zoology	Myonat	UK	Yes	No	Yes	Acoustic + visual observations
(Swift and Racey, 1983)	Journal of Zoology	Pleaur, Myodau	UK	Yes	Yes	Yes	Visual observations
(Thomas and Davison, 2022)	Ecology and Evolution	Myodau, Myonat, Myospp	UK	Yes	No	Yes	Acoustic + infra-red/camera traps/video
(Voortman and Bakker, 2020)	Deinsea	Pippip	Netherlands	Yes	No	Yes	Acoustic + visual observations

Bibliography:

- Ancillotto, L., Budinski, I., Nardone, V., Di Salvo, I., Della Corte, M., Bosso, L., Conti, P., Russo, D., 2018. What is driving range expansion in a common bat? Hints from thermoregulation and habitat selection. *Behavioural Processes* 157, 540–546. <https://doi.org/10.1016/j.beproc.2018.06.002>
- Bartonička, T., Bielík, A., Řehák, Z., 2008. Roost Switching and Activity Patterns in the Soprano Pipistrelle, *Pipistrellus pygmaeus*, during Lactation. *Annales Zoologici Fennici* 45, 503–512. <https://doi.org/10.5735/086.045.0605>
- Bartonička, T., Řehák, Z., 2004. Flight activity and habitat use of *Pipistrellus pygmaeus* in a floodplain forest. *Mammalia* 68, 365–375. <https://doi.org/10.1515/mamm.2004.036>
- Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. [https://doi.org/10.3161/1733-5329\(2007\)9\[527:TEOTIO\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2)
- Bullock, D.J., Combes, B.A., Eales, L.A., Pritchard, J.S., 1987. Analysis of the timing and pattern of emergence of the pipistrelle bat (*Pipistrellus pipistrettus*). *Journal of Zoology* 211, 267–274. <https://doi.org/10.1111/j.1469-7998.1987.tb01533.x>
- Catto, C.M.C., Racey, P.A., Stephenson, P.J., 1995. Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology* 235, 635–644. <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>
- Ciechanowski, M., Zajac, 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>
- Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for bat conservation: Part-night lighting and bats. *Anim Conserv* 18, 512–516. <https://doi.org/10.1111/acv.12200>
- DeCoursey, G., DeCoursey, P.J., 1964. Adaptive aspects of Activity Rhythms in Bats. *The Biological Bulletin* 126, 14–27. <https://doi.org/10.2307/1539413>
- Dietz, M., Kalko, E.K.V., 2007. Reproduction affects flight activity in female and male Daubenton's bats, *Myotis daubentonii*. *Can. J. Zool.* 85, 653–664. <https://doi.org/10.1139/Z07-045>
- Downs, N.C., Cresswell, W.J., Reason, P., Sutton, G., Wells, D., Williams, L., Wray, S., 2016. Activity patterns and use of night roosts by lesser horseshoe bats *Rhinolophus hipposideros* (Borkhausen, 1797). *Acta Chiropterologica* 18, 223–237. <https://doi.org/10.3161/15081109ACC2016.18.1.013>
- Duvergé, P.L., Jones, G., Rydell, J., Ransome, R.D., 2000. Functional significance of emergence timing in bats. *Ecography* 23, 32–40. <https://doi.org/10.1111/j.1600-0587.2000.tb00258.x>
- Encarnação, J.A., Kierdorf, U., Wolters, V., 2006. Seasonal variation in nocturnal activity of male Daubenton's bats, *Myotis daubentonii* (Chiroptera: Vespertilionidae). *Folia Zoologica- Praha* 55, 237–246.
- Entwistle, A.C., Racey, P.A., Speakman, J.R., 1996. Habitat exploitation by a gleaner bat, *Plecotus auritus*. *Phil. Trans. R. Soc. Lond. B* 351, 921–931. <https://doi.org/10.1098/rstb.1996.0085>

- García-Ruiz, I., Machado, M., Monsalve, M.Á., Monrós, J.S., 2017. Phenology of Emergence by Mediterranean Sympatric Cave-Dwelling Bats During Their Breeding Period. *Acta Chiropterologica* 19, 357–365. <https://doi.org/10.3161/15081109ACC2017.19.2.012>
- Gelhaus, M., Zahn, A., 2010. Roosting ecology, phenology and foraging habitats of a nursery colony of *Pipistrellus nathusii* in the southwestern part of its reproduction range. *Vespertilio* 13–14, 93–102.
- Goodenough, A.E., Deans, L., Whiteley, L., Pickering, S., 2015. Later is Better: Optimal Timing for Walked Activity Surveys for a European Bat Guild. *Wildlife Biology* 21, 323–328. <https://doi.org/10.2981/wlb.00131>
- Guixé, D., Roca, E., Barengueras, 2016. Time-lapse photography as an effective method for bat population monitoring. *Barb* 9. <https://doi.org/10.14709/BarbJ.9.1.2016.02>
- Hooker, J., Lintott, P., Stone, E., 2022. Lighting up our waterways: Impacts of a current mitigation strategy on riparian bats. *Environmental Pollution* 307, 119552. <https://doi.org/10.1016/j.envpol.2022.119552>
- Jenkins, E.V., Laine, T., Morgan, S.E., Cole, K.R., Speakman, J.R., 1998. Roost selection in the pipistrelle bat, *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae), in northeast Scotland. *Animal Behaviour* 56, 909–917. <https://doi.org/10.1006/anbe.1998.0858>
- Jones, G., Froidevaux, J.S.P., 2020. Soprano Pipistrelle *Pipistrellus pygmaeus* (Leach, 1825), in: Hackländer, K., Zachos, F.E. (Eds.), *Handbook of the Mammals of Europe*, *Handbook of the Mammals of Europe*. Springer International Publishing, Cham, pp. 1–25. https://doi.org/10.1007/978-3-319-65038-8_67-1
- Kapfer, G., Aron, S., 2007. Temporal variation in flight activity, foraging activity and social interactions by bats around a suburban pond. *Lutra* 50, 9–18.
- Lino, A., Fonseca, C., Mendes, G., Ramos Pereira, M.J., 2015. Roosting behaviour and phenology of the Lesser horseshoe bat (*Rhinolophus hipposideros*) in a breeding colony in Sintra, Portugal. *Galemys* 27, 1–12. <https://doi.org/10.7325/Galemys.2015.A1>
- Maier, C., 1992. Activity patterns of pipistrelle bats (*Pipistrellus pipistrellus*) in Oxfordshire. *Journal of Zoology* 228, 69–80. <https://doi.org/10.1111/j.1469-7998.1992.tb04433.x>
- 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. *Environmental Pollution* 305, 119267. <https://doi.org/10.1016/j.envpol.2022.119267>
- Marques, J.T., Rainho, A., Carapuço, M., Oliveira, P., Palmeirim, J.M., 2004. Foraging Behaviour and Habitat use by the European Free-Tailed Bat *Tadarida teniotis*. *Acta Chiropterologica* 6, 99–110. <https://doi.org/10.3161/001.006.0108>
- McAney, C.M., Fairley, J.S., 1988. Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at summer roosts. *Journal of Zoology* 216, 325–338. <https://doi.org/10.1111/j.1469-7998.1988.tb02433.x>
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>
- 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>
- Razgour, O., Hanmer, J., Jones, G., 2011. Using multi-scale modelling to predict habitat suitability for species of conservation concern: The grey long-eared bat as a case study.

- Biological Conservation 144, 2922–2930.
<https://doi.org/10.1016/j.biocon.2011.08.010>
- Robinson, M.F., Stebbings, R.E., 1997. Activity of the serotine bat, *Eptesicus serotinus*. *Myotis* 35, 5–16.
- Roeleke, M., Blohm, T., Kramer-Schadt, S., Yovel, Y., Voigt, C.C., 2016. Habitat use of bats in relation to wind turbines revealed by GPS tracking. *Sci Rep* 6, 28961.
<https://doi.org/10.1038/srep28961>
- Ruczyński, I., Zahorowicz, P., Borowik, T., Hałat, Z., 2017. Activity patterns of two syntopic and closely related aerial-hawking bat species during breeding season in Białowieża Primeval Forest. *Mamm Res* 62, 65–73. <https://doi.org/10.1007/s13364-016-0298-5>
- Rudolph, B.-U., Liegl, A., Von Helversen, O., 2009. Habitat Selection and Activity Patterns in the Greater Mouse-Eared Bat *Myotis myotis*. *Acta Chiropterologica* 11, 351.
<https://doi.org/10.3161/150811009X485585>
- Russo, D., Cistrone, L., Jones, G., 2007. Emergence time in forest bats: the influence of canopy closure. *Acta Oecologica* 31, 119–126. <https://doi.org/10.1016/j.actao.2006.11.001>
- Ružinská, R., Lóbbová, D., Kaňuch, P., 2022. Demographic characteristics shape patterns of dawn swarming during roost switching in tree-dwelling Daubenton's bat. *Sci Rep* 12, 10014. <https://doi.org/10.1038/s41598-022-14246-2>
- Rydell, J., Entwistle, A.C., 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>
- Shiel, C.B., Fairley, J.S., 1999. Evening emergence of two nursery colonies of Leisler's bat (*Nyctalus leisleri*) in Ireland. *Journal of Zoology* 247, 439–447.
<https://doi.org/10.1111/j.1469-7998.1999.tb01007.x>
- Shiel, C.B., Shiel, R.E., Fairley, J.S., 1999. Seasonal changes in the foraging behaviour of Leisler's bats (*Nyctalus leisleri*) in Ireland as revealed by radio-telemetry. *Journal of Zoology* 249, 347–358. <https://doi.org/10.1111/j.1469-7998.1999.tb00770.x>
- Stone, E.L., Jones, G., Harris, S., 2009. Street Lighting Disturbs Commuting Bats. *Current Biology* 19, 1123–1127. <https://doi.org/10.1016/j.cub.2009.05.058>
- Swift, S.M., 1997. Roosting and foraging behaviour of Natterer's bats (*Myotis nattereri*) close to the northern border of their distribution. *Journal of Zoology* 242, 375–384.
<https://doi.org/10.1111/j.1469-7998.1997.tb05809.x>
- Swift, S.M., 1980. Activity patterns of Pipistrelle bats (*Pipistrellus pipistrellus*) in north-east Scotland. *Journal of Zoology* 190, 285–295. <https://doi.org/10.1111/j.1469-7998.1980.tb01428.x>
- Swift, S.M., Racey, P.A., 1983. Resource partitioning in two species of vespertilionid bats (Chiroptera) occupying the same roost. *Journal of Zoology* 200, 249–259.
<https://doi.org/10.1111/j.1469-7998.1983.tb05787.x>
- Thomas, R.J., Davison, S.P., 2022. Seasonal swarming behavior of *Myotis* bats revealed by integrated monitoring, involving passive acoustic monitoring with automated analysis, trapping, and video monitoring. *Ecology and Evolution* 12.
<https://doi.org/10.1002/ece3.9344>
- Voortman, T., Bakker, G., 2020. Spatial and temporal variation in maternity roost site use of common pipistrelles *Pipistrellus pipistrellus* (Mammalia: Chiroptera) in Rotterdam. *Deinsea* 19, 1–16.

Appendix B: Acquisition and curation of biological data

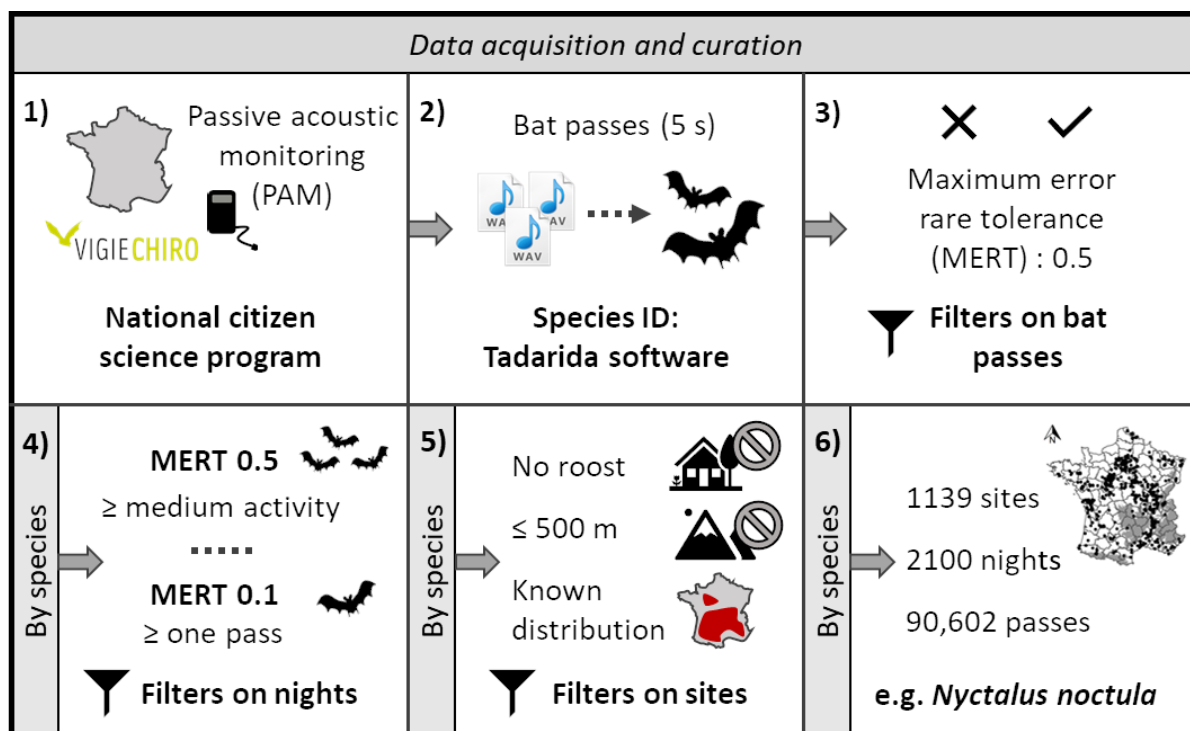


Fig. B.1: Schematic process of data acquisition (1-2) and curation (3-5), and example of final results for *Nyctalus noctula* (6).

1. Vigie-Chiro program

We used data from the “stationary points protocol” of the French citizen science bat monitoring program Vigie-Chiro which has been coordinated since 2014 by the French National Museum of Natural History (<https://www.vigienature.fr/fr/chauves-souris>) (Fig. B.1 1)). As part of this protocol, volunteers were asked to set up ultrasonic recorders on potential bat foraging sites for at least one full-night (from 30 min before sunset to 30 min after sunrise). All recorders had to be configured with recommended settings to limit heterogeneity between devices. Overall, we used data from 9807 nights monitored on 4409 sites (below 500 m above sea level, roosts excluded, see Appendix B 3) *Data curation*).

As this program was originally design to study bat population trends in France, the representativeness of the sample design was a major concern. When a volunteer wanted to participate to the “stationary points protocol”, he was thus encouraged to survey randomly sampled sites near a municipality that he had selected. He could also choose where he wanted to carry out the sampling sessions. To ensure that the sample of surveyed sites was

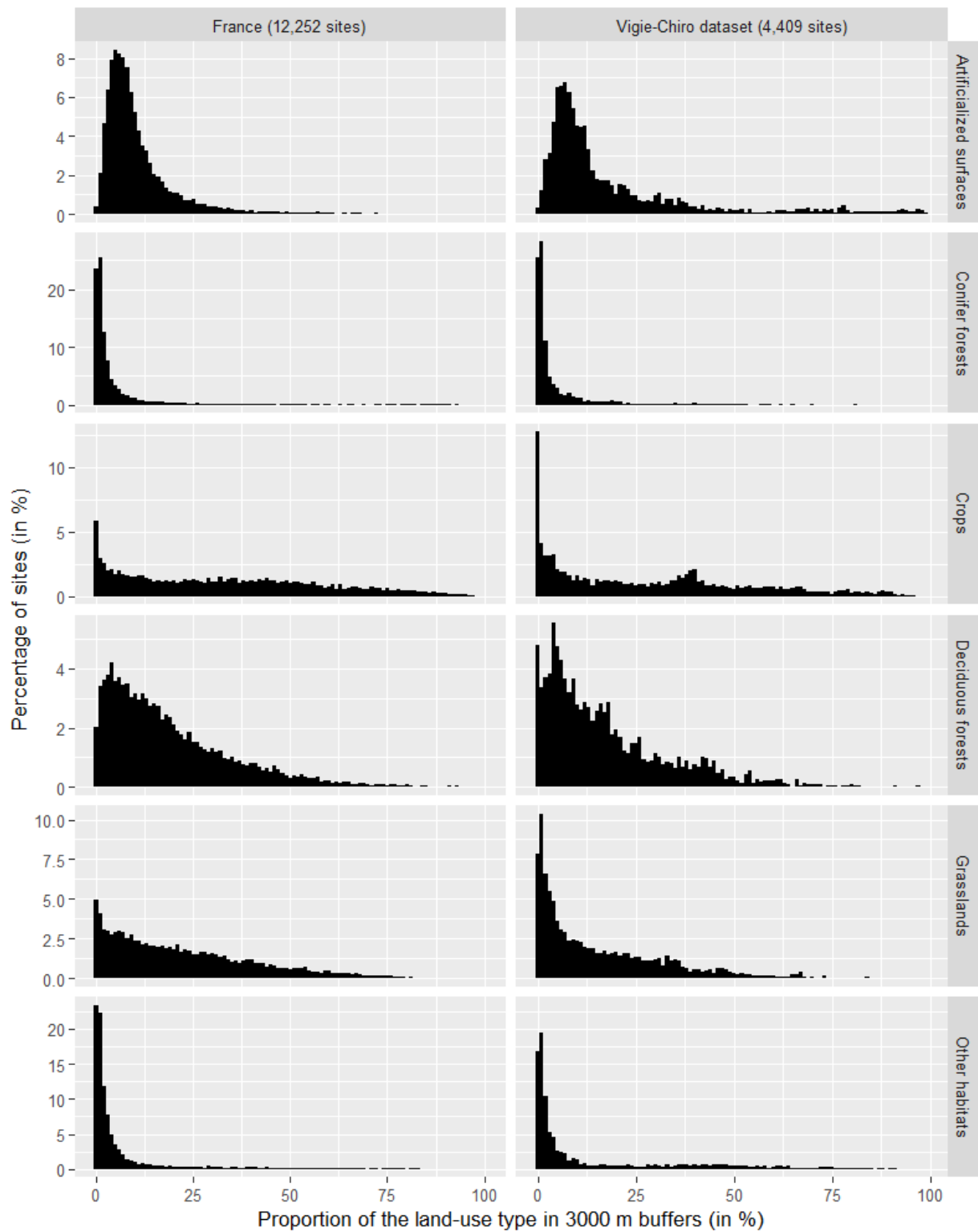


Fig. B.2: Gradients of the proportions of each land-use type in 3000 m buffer zones around randomly sampled sites in France (every 6000 m, below 500 m above sea level) and the sites of the Vigie-Chiro dataset (below 500 m above sea level)

representative of the distribution of habitats in France, we randomly sampled sites in a square grid (6000 m * 6000 m) in France and discarded sites that were above 500 m above sea level (as we only kept Vigie-Chiro sites that were below this altitude, see Appendix B 3) *Data curation*). For each of these randomly sampled sites (12,252), we extracted the proportion of each land-use type in 3,000 m buffer zones and compared it to the proportion of each land-use type in the buffer zones around the studied sites of our dataset. Overall, the buffer zones around the sites of our dataset covered the same gradients of land-use type as the buffer zones around sites randomly sampled in France (Fig. B.2).

Volunteers were asked to carry out the sampling sessions when weather conditions were relatively favourable for bats, i.e. no rain was forecasted, windspeed below 30 km.h⁻¹ (8.33 m.s⁻¹) and a relatively clement temperature at the beginning of the night (depending on the local context).

2. Species identification

Species identification was performed with the Tadarida software, which automatically detects and extracts sound parameters of recorded sound events (Figure B.1 2)). Using a random forest algorithm, it classifies them into classes according to a confidence index value (<https://github.com/YvesBas/Tadarida-C/>; Bas, Bas, & Julien, 2017). We considered bat passes, defined as the occurrence of a single or several bat calls during a 5-s interval (Millon et al., 2015) as a proxy for activity.

We discarded species for which there was not enough data (i.e. species that, after data curation, were found in less than 200 sites) and/or species for which we considered that automatic identification was not robust enough: *Eptesicus nilssonii*, *Myotis alcathoe*, *Myotis bechsteinii*, *Myotis brandtii*, *Myotis capaccinii*, *Myotis dasycneme*, *Myotis punicus*, *Nyctalus*

Table B.1: After data curation, by studied species: number of passes recorded, nights monitored and sites monitored. In the column “*Medium activity*”: medium activity thresholds in number of passes per night (Bas et al., 2020) used for data curation. In the column “*Departments*”: distribution range according to Arthur & Lemaire, (2015), the numbers are the official geographical codes of the French departments (see Figure B.3 for a spatial representation of the distribution range of each species according to Arthur & Lemaire, (2015)). Species are ranked according to their number of sites in the dataset after curation.

Species	Passes	Nights	Sites	Medium activity	Departments
<i>Pipistrellus pipistrellus</i>	5 700 561	7683	3658	41	<i>All France</i>
<i>Pipistrellus kuhlii</i>	1 965 676	5654	2732	18	Absent from: 52,54,57,59,88
<i>Nyctalus leisleri</i>	213 943	4984	2512	4	<i>All France</i>
<i>Eptesicus serotinus</i>	222 265	4299	2323	4	<i>All France</i>
<i>Myotis nattereri</i>	80 068	4056	2217	2	<i>All France</i>
<i>Barbastella barbastellus</i>	119 900	3651	1879	2	Absent from: 75,92,93,94,95
<i>Myotis daubentonii</i>	366 494	2248	1205	3	<i>All France</i>
<i>Rhinolophus ferrumequinum</i>	60 765	2076	1187	1	Absent from: 59,67,75,78, 92,93,94
<i>Plecotus austriacus</i>	28 916	1909	1164	2	<i>All France</i>
<i>Nyctalus noctula</i>	90 602	2100	1139	3	Absent from: 2A,2B
<i>Rhinolophus hipposideros</i>	36 173	1842	1097	1	Absent from: 59,75,78,91, 92,93,94
<i>Pipistrellus pygmaeus</i>	625 166	1895	1011	8	Absent from: 23,53,61,70,71
<i>Pipistrellus nathusii</i>	136 276	1822	958	7	Absent from: 32
<i>Myotis emarginatus</i>	17 099	1481	911	2	Absent from: 75,92,93,94
<i>Myotis mystacinus</i>	85 893	1492	862	4	<i>All France</i>
<i>Hypsugo savii</i>	53 694	1292	783	4	Present in: 01,03,04,05,06, 07,09,11,12,13,15,16,19,24, 25,26,2A,2B,30,31,33,34,36, 38,39,42,43,46,47,48,55,63, 64,65,66,69,73,74,81,82,83, 84,90
<i>Myotis myotis/blythii</i>	7746	1127	783	1	Absent from: 2A,2B,75,92, 93,94
<i>Miniopterus schreibersii</i>	26 848	1343	776	2	Absent from: 02,08,14,27, 28,29,45,50,51,58,59,60,61, 62,67,75,76,77,78,80,90,91, 92,93,94,95
<i>Tadarida teniotis</i>	87 988	926	568	4	Present in: 01,04,05,06,07, 09,11,12,13,15,25,26,2A,2B, 30,31,34,38,39,42,43,46,48, 64,65,66,69,70,73,74,81,82, 83,84
<i>Plecotus auritus</i>	2965	290	226	1	Absent from: 2A,2B

lasiopterus, *Plecotus macrobullaris*, *Rhinolophus euryale*, *Rhinolophus mehelyi* and *Vespertilio murinus*. We chose to keep *Myotis blythii* and *Myotis myotis* despite their high acoustic similarity (Barataud and Tupinier, 2020) by grouping them in a class named Great *Myotis*. Eventually, we focused on 20 species or group of species (Table B.1).

3. Data curation

We only kept passes whose confidence index value was greater than 0.5, to obtain, for each species, a maximum error rate tolerance of 0.5 (minimisation of false positives while keeping a high number bat passes, Barré et al., 2019) (Figure B.1 3)). For each species, we retained only the monitored nights with (1) at least one pass of the species with a high confidence index value (maximum error rate tolerance greater than or equal to 0.1), (2) at least a medium activity. The thresholds used to characterise the level of activity for each species were those of the national reference scale developed with the Vigie-Chiro dataset (the quantile 0.25 of the total number of this species' passes per night being the threshold for having at least a medium activity, Table B.1) (Bas et al., 2020) (Figure B.1 4)). The objective of these filters was to consider only the sampling sessions during which the presence of the species was highly probable and high enough to be studied.

To avoid bias due to specific diel activity patterns near bat roosts (e.g. earlier activity at the beginning of the night), we excluded sampling sessions carried out near potential bat roosts. We also discarded surveys carried out in mountain environments (defined as sites above 500 m above sea level) to avoid biases due potential particular behaviours in such environments (Cryan et al., 2000; McCain, 2007). To discard some of the remaining false positives, for each species, we excluded sites that were outside their known distribution range according to Arthur & Lemaire (2015) (Table B.1, Figure B.3) (Figure B.1 5)). To ensure result robustness against automated identification errors that could persist despite the precautions we took when filtering data, we chose to follow the approach of Barré et al. (2019) (Appendix C). We showed that our results were not sensitive to the error rates considered and were robust against automated identification errors.

The total number of passes, nights and sites eventually studied by species are presented Table B.1.

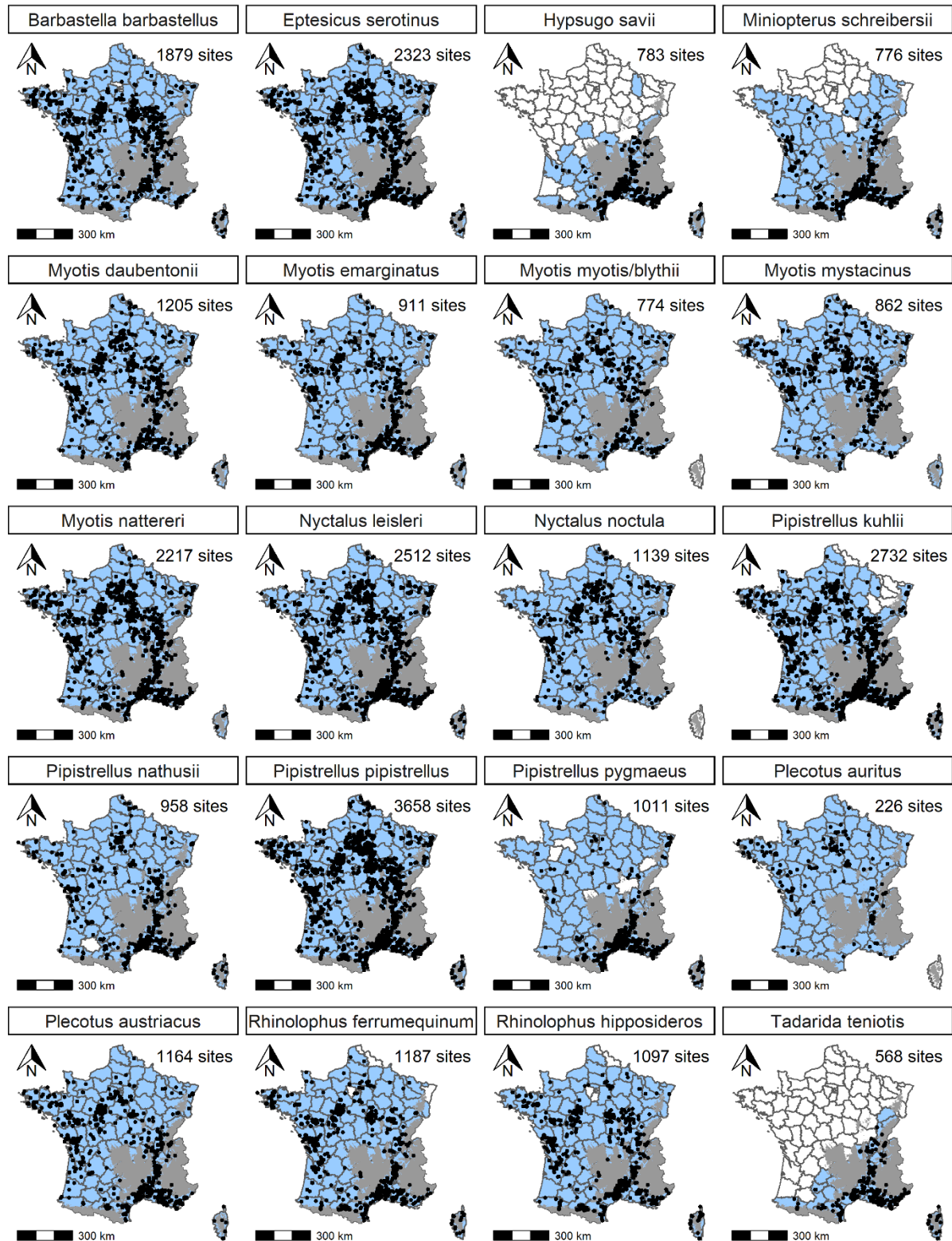


Fig. B.3: Sites monitored by species (black dots) after data curation. In grey, mountain environments (defined as areas above 500 m above sea level), sites in these areas were discarded. In white, French departments where the species is absent (has never been found) according to Arthur & Lemaire (2015), sites in these departments were discarded. In blue, departments where the species has been found at least once according to Arthur & Lemaire (2015) (including departments where the species may have disappeared since, departments where the species is present but little known, departments where the species is exceptionally observed, departments where the species is rare or fairly rare, departments where the species is uncommon or locally common and departments where the species is fairly common to very common).

Bibliography:

- Arthur, L., Lemaire, M., 2015. Les chauves-souris de France, Belgique, Luxembourg et Suisse. Biotope ; Museum national d'Histoire Naturelle, Mèze; Paris.
- Barataud, M., Tupinier, Y., 2020. Écologie acoustique des chiroptères d'Europe: identification des espèces, étude de leurs habitats et comportements de chasse, 4th ed, Inventaires & biodiversité. Biotope éditions Muséum national d'histoire naturelle, Mèze Paris.
- Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S.E., Julien, J.-F., Claireau, F., Kerbirou, C., Bas, Y., 2019. Accounting for automated identification errors in acoustic surveys. *Methods Ecol Evol* 10, 1171–1188. <https://doi.org/10.1111/2041-210X.13198>
- 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>
- Bas, Y., Kerbirou, C., Roemer, C., Julien, J.-F., 2020. Bat reference scale of activity levels (Version 2020-04-10) [refPF_Total_2020-04-10.csv] [WWW Document]. Team-Chiro. URL <https://croemer3.wixsite.com/teamchiro/reference-scales-of-activity> (accessed 7.20.22).
- Cryan, P.M., Bogan, M.A., Altenbach, J.S., 2000. Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy* 81, 719–725. [https://doi.org/10.1644/1545-1542\(2000\)081<0719:EOEODO>2.3.CO;2](https://doi.org/10.1644/1545-1542(2000)081<0719:EOEODO>2.3.CO;2)
- McCain, C.M., 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecol Biogeography* 16, 1–13. <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1466-8238.2006.00263.x>
- Millon, L., Julien, J.-F., Julliard, R., Kerbirou, C., 2015. Bat activity in intensively farmed landscapes with wind turbines and offset measures. *Ecological Engineering* 75, 250–257. <https://doi.org/10.1016/j.ecoleng.2014.11.050>

Appendix C: Robustness of the automated identification

As the confidence in the automated identification is an important issue in such a study, we provide in this appendix additional information on the robustness of the identification.

Firstly, Tadarida-C (i.e. the software module of the Tadarida toolbox which handles the classification of all detected sound events, Bas et al., 2017) is now integrating a contextual classifier in addition to classification based on acoustic features. It uses similar random forest algorithms as those in Metcalf et al., (2022) and is trained over more than 90,000 bat occurrences in recording files. Like in Metcalf et al., (2022), this greatly reduces error rates (by a factor of three) by taking into account the relative abundance of each species during the night, and the distribution of confidence scores among detection events.

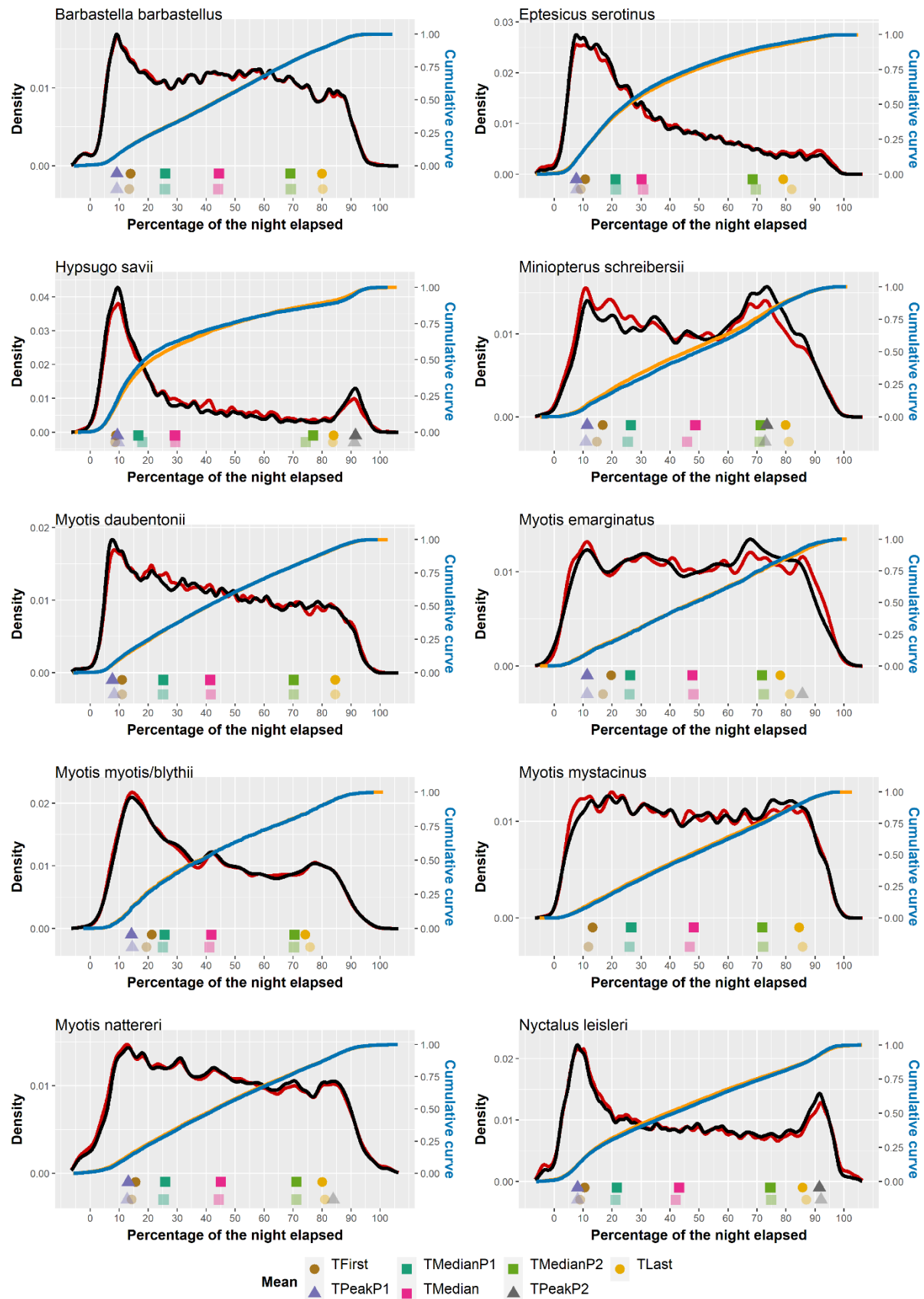
Secondly, several filters applied to the dataset during the data curation (detailed in Appendix B) were designed to reduce the number of false positives per species as much as possible. By applying these filters, we considerably reduced the number of bat passes, nights and sites for species whose identification through Tadarida was not robust enough. These species therefore ended up not being considered as they were found in less than 200 sites after data curation.

Eventually, to ensure the robustness of the results against automated identification errors that could persist despite the precautions we took when filtering and analysing the data, we chose to follow the approach of Barré et al. (2019). For each species, this consisted in comparing:

- (1) the results we obtained with a maximum error rate tolerance (MERT) of 0.5 which minimises false positives while keeping a high number of bat passes (*main analyses in the manuscript*)
- (2) with the results we obtained with a MERT of 0.1 which limits false positives but discards more true positives.

As shown in Fig. C.1, the results are highly consistent whether we used a MERT of 0.5 or a MERT of 0.1. This confirms that our results are not sensitive to the error rates considered and are robust against automated identification errors.

Appendices – Appendix I



Appendices – Appendix I

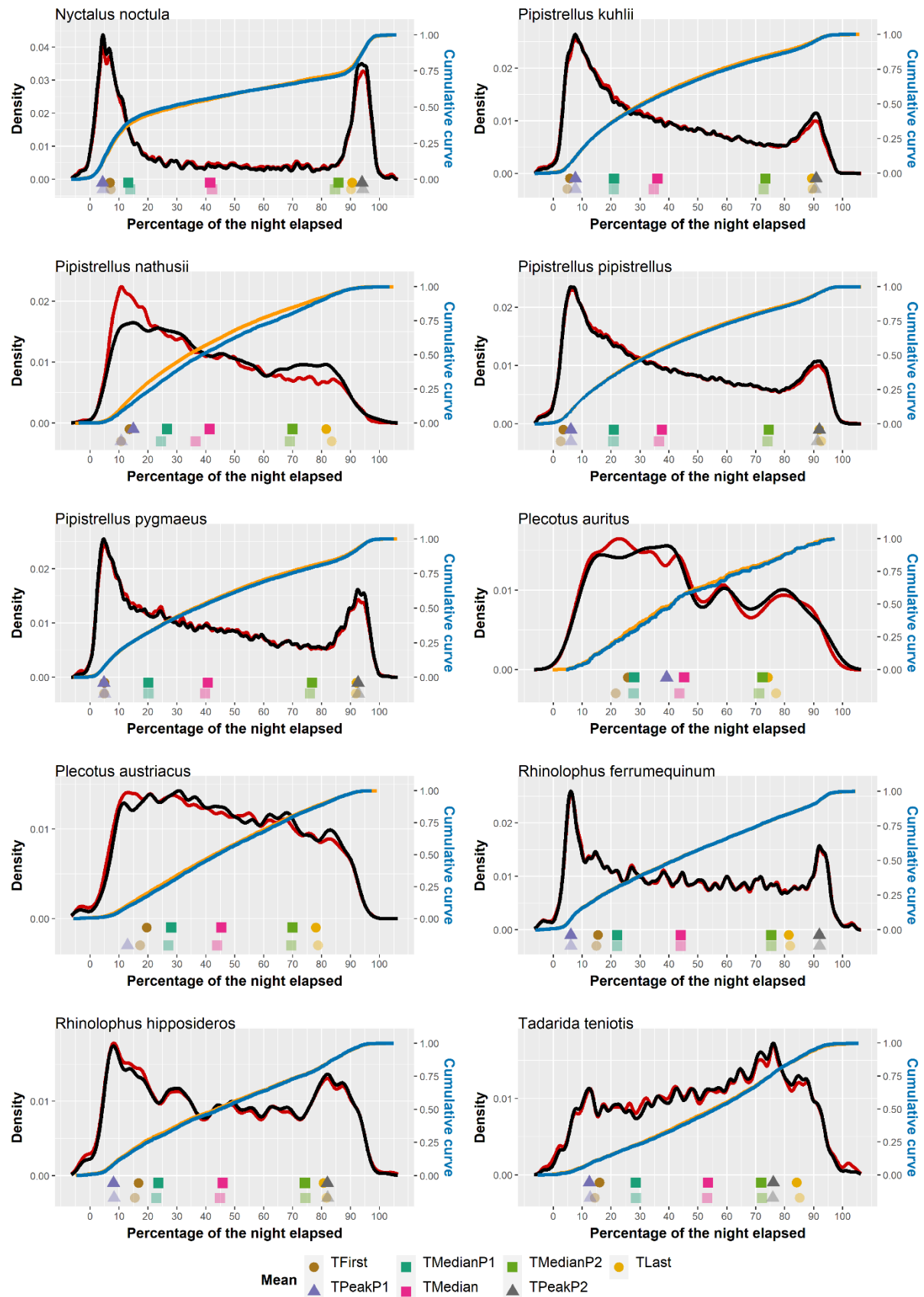


Fig. C.1: Comparison of the results obtained with a MERT of 0.1 and a MERT of 0.5 for each species studied. In black and red, estimated density of activity according to the percentage of the night elapsed with a MERT of 0.1 and of 0.5 respectively. In blue and orange, cumulative curve of weighted bat activity with a MERT of 0.1. and 0.5 respectively. The symbols represent the mean times of the key descriptors and the times of the activity peaks detected. The top symbols are for a MERT of 0.1 and the lighter symbols at the bottom are for a MERT of 0.5.

Bibliography:

- Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S.E., Julien, J.-F., Claireau, F., Kerbiriou, C., Bas, Y., 2019. Accounting for automated identification errors in acoustic surveys. *Methods Ecol Evol* 10, 1171–1188. <https://doi.org/10.1111/2041-210X.13198>
- 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>
- Metcalf, O.C., Barlow, J., Bas, Y., Berenguer, E., Devenish, C., França, F., Marsden, S., Smith, C., Lees, A.C., 2022. Detecting and reducing heterogeneity of error in acoustic classification. *Methods Ecol Evol* 13, 2559–2571. <https://doi.org/10.1111/2041-210X.13967>

Appendix D: Additional information on the methods designed to characterise and compare bat diel activity patterns

1. Key descriptors

To compute the times of the key descriptors, we had to consider the hierarchical structure of our dataset. Monitored sites were composed of one or several monitored nights during which bat passes were recorded. Hence, we applied the following workflow for each species:

- (i) **By night** (kept for the species after data curation): we calculated the times of the five key descriptors.
- (ii) **By site**: if there were several monitored nights, we calculated a mean time by site for each key descriptor. We postulated that the more passes of a species during a night there are, the more robust the estimation of the times of the key descriptors. We hence calculated the following weighted mean:

$$descr_j = \sum_{i=1}^{N_j} descr_{i,j} \times descr_{j,i} \quad (\text{Eq D.1})$$

With:

$$weight_{j,i} = \frac{\log(1 + P_{j,i})}{\sum_{i=1}^{N_j} \log(1 + P_{j,i})} \quad (\text{Eq D.2})$$

With:

j = site ID; **i** = i^{th} night of a site;

drscr_j = “mean” time of a given key descriptor at the site_j;

descr_i = time of a given key descriptor during the i^{th} night of the site_j;

N_j = number of surveyed nights at the site_j, **P_{j,i}** = number of passes of the night_{i,j}

- (iii) **Over the whole dataset**: we calculated a weighted mean of the mean time of the key descriptors by site based on the number of passes by site. We hence had to define the mean number of passes by site, to reflect the weight applied on the calculation of the times of the key descriptors, we defined it as follows:

$$P_j = [\sum_{i=1}^{N_j} P_{j,i} \times \log(1 + P_{j,i})] / [\sum_{i=1}^{N_j} \log(1 + P_{j,i})] \quad (\text{Eq D.3})$$

With:

j = site ID; **i** = i^{th} night of a site; **P_j** = “mean” number of passes of the site_j;

P_{j,i} = number of passes of the night_{i,j}; **N_j** = number of surveyed nights at the site_j

We then calculated the following weighted mean:

$$descr = \sum_{j=1}^S descr_j \times weight_j \quad (\text{Eq D.4})$$

With:

$$weight_j = \frac{\log(1 + P_j)}{\sum_{j=1}^S \log(1 + P_j)} \quad (\text{Eq D.5})$$

With:

j = site ID; **descr** = “mean” time of a given key descriptor over the whole dataset;

descr_j = “mean” time of a given key descriptor at the site_j; **S** = number of sites;

P_j = “mean” number of passes of the site_j

2. Activity distribution throughout the night

To characterise the activity distribution throughout the night of each species, we estimated a density of activity (kernel density estimates, R function *density*). In previous studies (e.g. Day et al., 2015; Newson et al., 2015), some authors considered the number of bat passes during given time periods (e.g. every hours, every 15 min). In comparison, density estimation better accounted for the continuous aspect of our data. We chose a Gaussian smoothing kernel and the data-based bandwidth selection method proposed by Sheather and Jones (1991) which has been widely recommended for its overall good performance (Sheather, 2004). We used the default setting ($n = 512$) for the number of equally spaced time points at which the density was to be estimated, ranging from the time of the earliest bat pass in our dataset to the latest (i.e. from about -7 to 106 % of the night elapsed).

To estimate the activity distribution throughout the night of a given species, we used all its passes kept after data curation as, for rare species particularly, there were not enough passes by night to characterise their activity distribution by night. We had to account for the hierarchical structure of our dataset so that, for instance, the activity distribution throughout the night would not be based on a few nights with many passes or a few sites with many monitored nights. Thus, we attributed a weight to each pass so that:

- (i) a site weight (Eq C.5) in the density calculation would be based on the mean number of passes of that site (Eq C.3),
- (ii) a night weight inside a site (Eq C.2) would be based on the number of passes during this night,
- (iii) each pass of a given night in a given site would have the same weight.

Eventually each pass weight in the density calculation was calculated as follows:

$$\text{weight}_{j,i,k} = \frac{\text{weight}_{j,i} \times \text{weight}_j}{P_{j,i}} \quad (\text{Eq D.6})$$

With:

j = site ID; **i** = i^{th} night of a site; **k** = k^{th} pass in a night; **P_{j,i}** = number of passes of the night_{j,i}
weight_{j,i,k} = weight of the k^{th} pass of the i^{th} night of the site_j in the density estimation;
weight_j = see (Eq C.5); **weight_{j,i}** = see (Eq C.2)

We constructed 95% confidence bands for the estimated densities using bootstrap. We computed 1000 resamples – with replacement – of as many sites as in the original dataset for each species. For the 1000 resamples, we estimated the density of activity with the same parameters as above (the weight of each pass being updated according to the resample considered). The lower limit of the confidence band was then defined as the value of the quantile 0.025 of all these resamples at each time points (as a reminder: 512 equally spaced time points between -7 to 106 % of the night elapsed) and the upper limit as the value of the quantile 0.095.

To detect the times of the activity peaks based on the estimated density of activity (TPeakP1 for peaks occurring during the first part of the night, TPeakP2 for peaks occurring during the second part):

- (i) We detected local maxima in a window equivalent to a quarter of the night (169 time points) around time points for which the density was estimated (with reflecting boundary condition).
- (ii) We calculated a peak score for each time point as follows:

$$\text{peak score}_x = \text{density}_x - \text{mean (density of the temporal neighbours)} \quad (\text{Eq D.7})$$

With:

x = a time point for which the density of activity was estimated;

density_x = the density of activity estimated at x;

temporal neighbours = temporal window equal to a quarter of the night around x (i.e. 64 time points to the left and the right of x, with reflecting boundary condition).

- (iii) We detected time points that corresponded to the times of local density maxima and whose peak score was greater than the quantile 0.9 of all the peak scores (R package *scorepeak* (Ochi, 2019)).

We calculated a cumulative curve of weighted bat activity throughout the night using the cumulative weight of all passes ranked by increasing percentage of the night elapsed. For a given time period during the night (starting at time 1 and ending at time 2), the value of the cumulative curve at time 2 minus the value of the cumulative curve at time 1 corresponded to the percentage of weighted bat passes occurring during this time period in our dataset, hereafter called percentage of weighted activity.

To assess whether the weighted activity of a species was concentrated around activity peaks or more evenly distributed throughout the night, we searched for the 15 % interval of the night during which its weighted activity was maximum. To do this, we considered each pass of this species and we calculated the percentage of its weighted activity occurring during the 15 % interval of the night starting from the time of that pass. If the weighted activity was evenly distributed throughout the night, the maximum percentage of weighted activity occurring during a 15 % interval of the night would be close to 15 %. If the weighted activity was concentrated around peaks, the maximum percentage of weighted activity occurring during a 15 % interval of the night would be much higher than 15 % and this 15 % interval of the night would cover the time of an activity peak.

3. Clustering of the species

To determine whether species could be grouped according to similarities in their diel activity patterns, we performed a Hierarchical Clustering on the Principal Components (HCPC) of a Principal Component Analysis (PCA) (R package *FactoMineR* (Lê et al., 2008)) using the times of the key descriptor and the times of the activity peaks. As we did not detect activity peaks for some species (during the first part of the night and/or the second part), we imputed the missing values with the PCA model, so that the imputed values had no weight on the results of the PCA (R package *missMDA* (Josse and Husson, 2016)). We compared the average of each variable (mean time of key descriptors and times of activity peaks) for the species in each cluster with the overall average (i.e. the average for all species studied). We tested whether the average in each cluster was equal to the overall average (see test in Husson et al., 2010, 2009).

Bibliography:

- Day, J., Baker, J., Schofield, H., Mathews, F., Gaston, K.J., 2015. Part-night lighting: implications for bat conservation: Part-night lighting and bats. *Anim Conserv* 18, 512–516. <https://doi.org/10.1111/acv.12200>
- Husson, F., Josse, J., Pagès, J., 2010. Principal component methods-hierarchical clustering-partitional clustering: why would we need to choose for visualizing data? (Technical Report of the Applied Mathematics Department). Agrocampus.
- Husson, F., Lê, S., Pagès, J., 2009. *Analyse de données avec R*, 1st ed, *Pratique de la statistique*. Presses universitaires de Rennes, Rennes.
- Josse, J., Husson, F., 2016. **missMDA**: A Package for Handling Missing Values in Multivariate Data Analysis. *J. Stat. Soft.* 70, 1–31. <https://doi.org/10.18637/jss.v070.i01>
- Lê, S., Josse, J., Husson, F., 2008. **FactoMineR**: An *R* Package for Multivariate Analysis. *J. Stat. Soft.* 25, 1–18. <https://doi.org/10.18637/jss.v025.i01>
- Newson, S.E., Evans, H.E., Gillings, S., 2015. A novel citizen science approach for large-scale standardised monitoring of bat activity and distribution, evaluated in eastern England. *Biological Conservation* 191, 38–49. <https://doi.org/10.1016/j.biocon.2015.06.009>
- Ochi, S., 2019. scorepeak: Peak Functions for Peak Detection in Univariate Time Series.
- Sheather, S.J., 2004. Density Estimation. *Statist. Sci.* 19. <https://doi.org/10.1214/088342304000000297>
- Sheather, S.J., Jones, M.C., 1991. A Reliable Data-Based Bandwidth Selection Method for Kernel Density Estimation. *Journal of the Royal Statistical Society: Series B (Methodological)* 53, 683–690. <https://doi.org/10.1111/j.2517-6161.1991.tb01857.x>

Table E: Mean time of the key descriptor s and time of the activity peaks in percentage of the night elapsed. Species are named with their species codes (correspondence between codes and full Latin and English names in Table F). Species are ranked by increasing value of TFirst. “Sd” is the weighted standard deviation of the times of the key descriptors calculated by site. For TFirst and TMedianP1, the ealier the time, the yellower the cell, and the later the time, the greyer the cell. For TLast and TMedianP2, the later the time, the yellower the cell, and the earlier the time, the greyer the cell. The clusters into which the species were classified according to the HCPC (C: crepuscular species, I: intermediate species, D: late species) are in the column “Cl.”.

Species	Cl.	TFirst		TPeakP1	TMedianP1		TMedian		TMedianP2		TPeakP2	TLast	
		Mean	Sd	/	Mean	Sd	Mean	Sd	Mean	Sd	/	Mean	Sd
Pippip	C	2.55	4.33	6.06	20.81	8.95	36.55	18.39	74.08	10.19	91.34	92.56	7.08
Pipkuh	I	4.84	4.77	7.61	20.94	9.31	34.73	18.77	72.74	10.56	90.45	89.58	7.85
Pippyg	C	4.89	5.44	4.96	20.20	9.68	39.82	20.75	75.97	11.51	92.66	91.82	7.52
Nycnoc	C	7.14	8.42	4.52	13.86	10.96	42.12	32.94	84.70	12.35	94.21	90.24	10.11
Hypsav	I	8.58	6.55	9.60	17.93	9.87	29.34	20.86	74.32	12.51	91.12	83.67	11.71
Nyclei	I	8.98	8.59	8.05	21.16	11.10	42.02	23.86	74.89	11.84	92.00	86.99	10.66
Eptser	I	9.12	7.00	7.83	21.27	9.83	30.72	17.77	69.60	11.01	NA	81.94	11.66
Pipnat	I	10.68	6.42	10.70	24.47	9.37	36.41	17.17	68.97	9.01	NA	83.54	9.26
Myodau	I	10.99	8.69	8.27	25.12	9.61	41.60	17.70	70.22	8.84	NA	84.51	9.74
Myomys	L	11.78	9.08	NA	26.01	10.35	46.86	19.46	72.03	9.63	NA	85.68	8.90
Barbar	L	13.50	9.84	9.16	25.75	10.99	44.21	18.85	69.23	9.69	NA	80.28	10.44
Myonat	L	14.26	10.97	12.69	25.29	10.73	44.30	19.54	71.16	10.30	83.83	80.96	11.28
Tadten	L	14.38	11.58	12.69	28.58	11.49	53.21	20.51	72.15	9.99	75.87	85.19	10.68
Minsch	L	14.71	9.60	10.92	25.42	10.18	45.95	19.00	70.92	9.12	72.78	80.96	10.09
Rhifer	I	14.95	12.54	6.06	22.07	12.56	44.07	24.47	75.34	12.53	92.00	81.89	13.26
Rhihip	L	15.44	12.01	8.27	22.90	12.04	44.89	23.49	74.41	10.79	82.06	81.66	11.63
Myoema	L	16.89	11.50	11.36	25.98	11.21	48.11	20.51	72.32	10.29	85.59	81.29	11.23
Pleaus	L	17.33	10.89	12.91	27.00	10.84	43.81	19.02	69.52	9.86	NA	78.76	11.00
MyoGS	L	19.43	10.50	14.46	25.07	10.59	41.09	21.13	70.31	10.30	NA	75.87	11.24
Pleaur	L	21.61	12.17	NA	27.77	10.25	43.64	21.36	71.15	11.94	NA	77.03	12.94

Table F: Correspondence between species codes (first three letters of the Latin genus name and first three letters of the Latin species name) and Latin and English full names.

Species code	Latin name	English name
Barbar	<i>Barbastella barbastellus</i>	Western barbastelle
Eptser	<i>Eptesicus serotinus</i>	Serotine bat
Hypsav	<i>Hypsugo savii</i>	Savi's pipistrelle
Minsch	<i>Miniopterus schreibersii</i>	Common bent-wing bat
Myodau	<i>Myotis daubentonii</i>	Daubenton's bat
Myoema	<i>Myotis emarginatus</i>	Geoffroy's bat
MyoGS	<i>Myotis myotis/blythii</i>	Great <i>myotis</i>
- Myomyo	- <i>Myotis myotis</i>	- Greater mouse-eared bat
- Myobly	- <i>Myotis blythii</i>	- Lesser mouse-eared bat
Myomys	<i>Myotis mystacinus</i>	Whiskered bat
Myonat	<i>Myotis nattereri</i>	Natterer's bat
Nyclei	<i>Nyctalus leisleri</i>	Lesser noctule
Nycnoc	<i>Nyctalus noctula</i>	Common noctule
Pipkuh	<i>Pipistrellus kuhlii</i>	Kuhl's pipistrelle
Pipnat	<i>Pipistrellus nathusii</i>	Nathusius's pipistrelle
Pippip	<i>Pipistrellus pipistrellus</i>	Common pipistrelle
Pippyg	<i>Pipistrellus pygmaeus</i>	Soprano pipistrelle
Pleaur	<i>Plecotus auritus</i>	Brown long-eared bat
Pleaus	<i>Plecotus austriacus</i>	Grey long-eared bat
Rhifer	<i>Rhinolophus ferrumequinum</i>	Greater horseshoe bat
Rhihip	<i>Rhinolophus hipposideros</i>	Lesser horseshoe bat
Tadten	<i>Tadarida teniotis</i>	European free-tailed bat

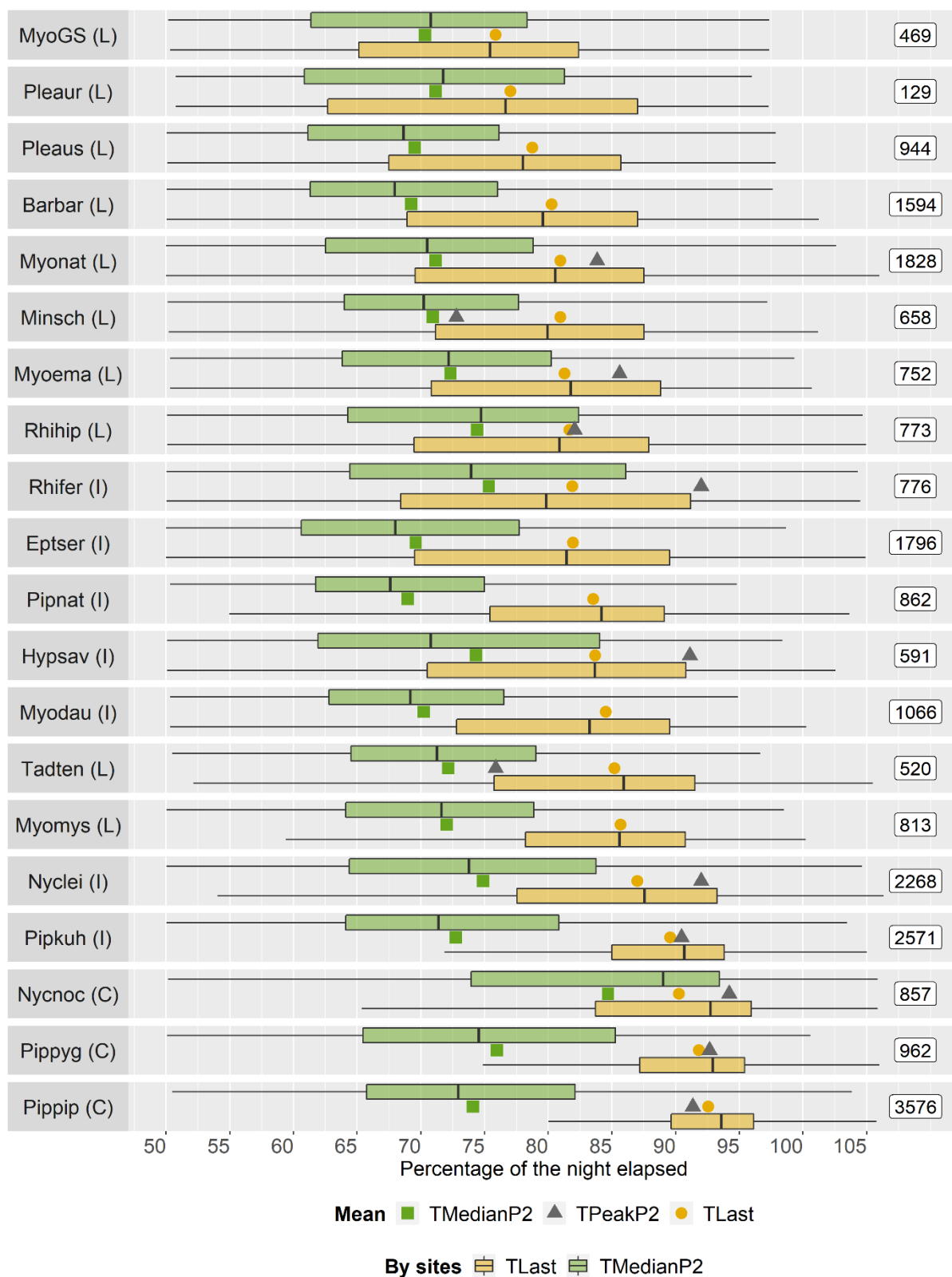
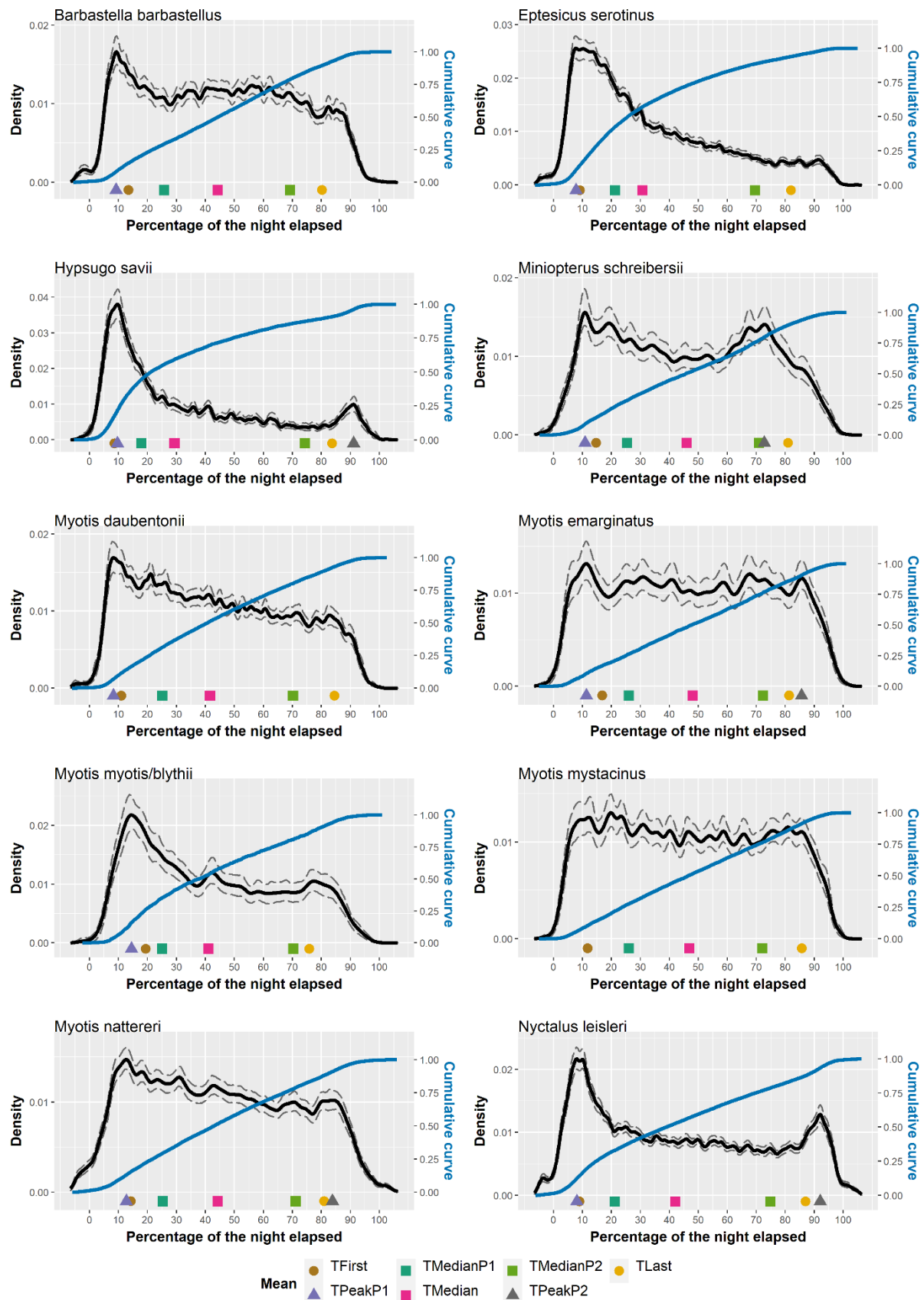


Fig. G: TLast, TPeakP2 and TMedianP2 for each bat species. On the left are the codes of the species studied (correspondence between the codes and the full Latin and English names in Table F), followed by the cluster in which they were classified according to the HCPC (C: crepuscular species, I: intermediate species, L: late species). On the right is the number of sites by species. Species are ranked by increasing value of mean TLast.

Appendices – Appendix I



Appendices – Appendix I

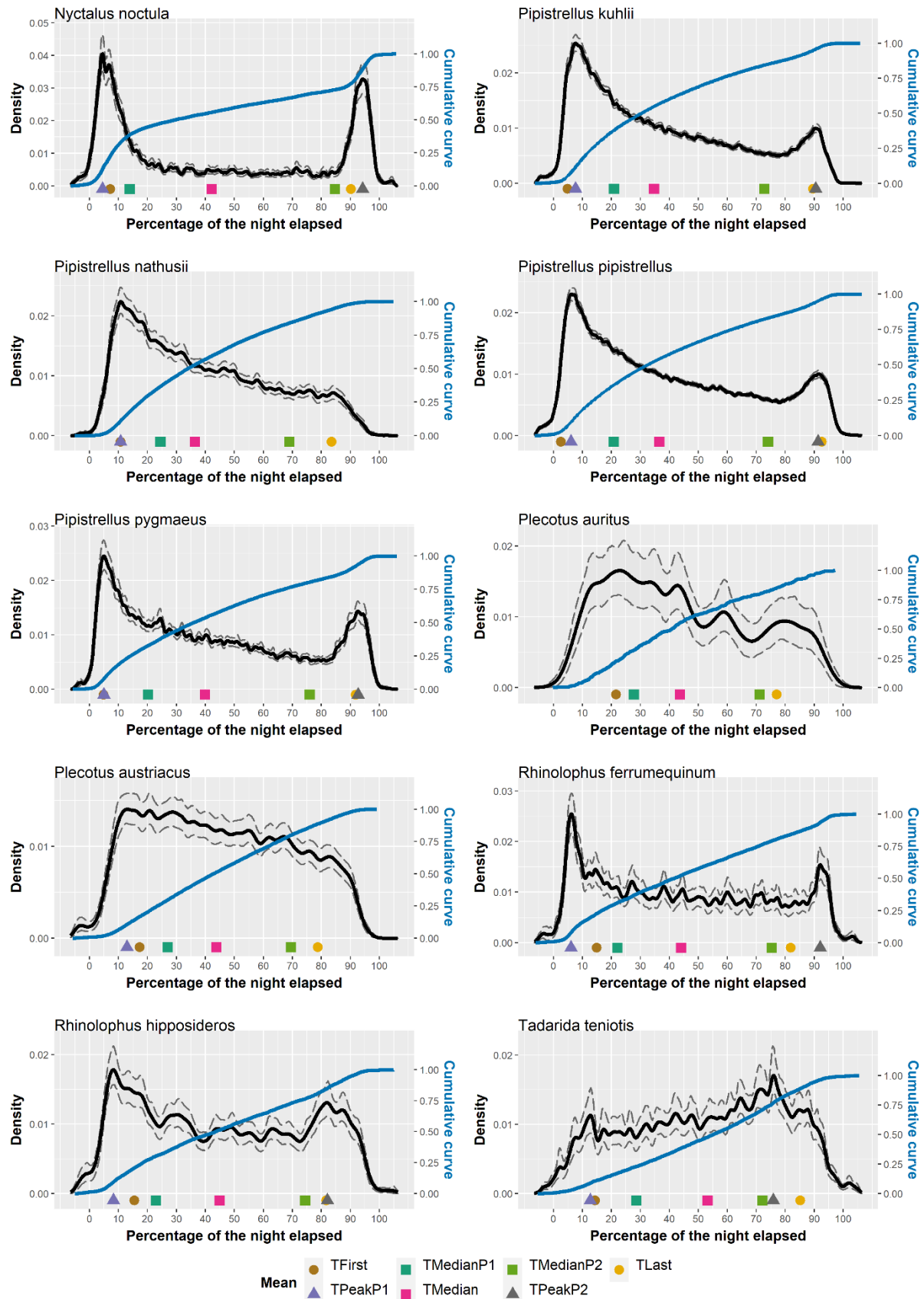


Fig. H: Activity distribution throughout the night for the twenty species studied: in black, estimated density of activity according to the percentage of the night elapsed. In blue, cumulative curve of weighted bat activity. The dashed lines represent the 95 % confidence bands for the estimated density. Symbols represent the mean times of the key descriptors and the times of the activity peaks detected.

Table I: Descriptive metrics on bat activity distribution throughout the night: “Activity 15%” is the maximum percentage of weighted activity in a 15 % interval of the night. “Interval 15 %” is the lower and upper limits (in percentage of the night elapsed) of the 15 % interval of the night during which the percentage of weighted activity was equal to “Activity 15%”. “Activity before 10 %” and “Activity after 90 %” correspond to the percentage of weighted activity occurring before 10 % of the night had elapsed and after 90 % of the night had elapsed respectively. Correspondence between the codes and the full Latin and English names can be found in Table F. Species are ranked by increasing “Activity 15 %”.

Species	Activity 15 %	Interval 15 %	TFPeak	Activity before 10 %	Activity after 90 %
Hypsav	43.1	[4.0 , 19]	9.6	23.0	4.9
Nycnoc	38.3	[0.6 , 15.6]	4.5	31.3	22.8
Eptser	35.7	[5.3 , 20.3]	7.8	16.7	2.8
Pipkuh	31.5	[3.8 , 18.8]	7.6	17.7	4.7
Pipnat	29.2	[6.7 , 21.7]	10.7	9.4	1.7
MyoGS	29.0	[8.8 , 23.8]	14.5	6.5	1.4
Pippip	28.2	[3.1 , 18.1]	6.1	18.2	6.2
Pippyg	26.9	[2.3 , 17.3]	5.0	18.7	9.9
Nyclei	26.0	[3.8 , 18.8]	8.1	16.5	9.1
Pleaur	24.7	[11.6 , 26.6]	NA	4.2	3.5
Rhifer	24.6	[3.8 , 18.8]	6.1	16.0	9.2
Rhihip	23.4	[5.1 , 20.1]	8.3	12.5	5.4
Myodau	22.4	[6.3 , 21.3]	8.3	9.9	2.5
Tadten	21.6	[63.7 , 78.7]	12.7	6.0	5.5
Minsch	21.2	[8.2 , 23.2]	10.9	7.2	2.8
Barbar	20.9	[5.9 , 20.9]	9.2	9.7	1.8
Pleaus	20.6	[10.7 , 25.7]	12.9	6.5	2.2
Myonat	20.2	[7.5 , 22.5]	12.7	9.3	3.3
Myomys	18.5	[9.0 , 24]	NA	8.4	4.2
Myoema	17.4	[4.2 , 19.2]	11.4	8.3	4.6

Appendix J: Clustering results

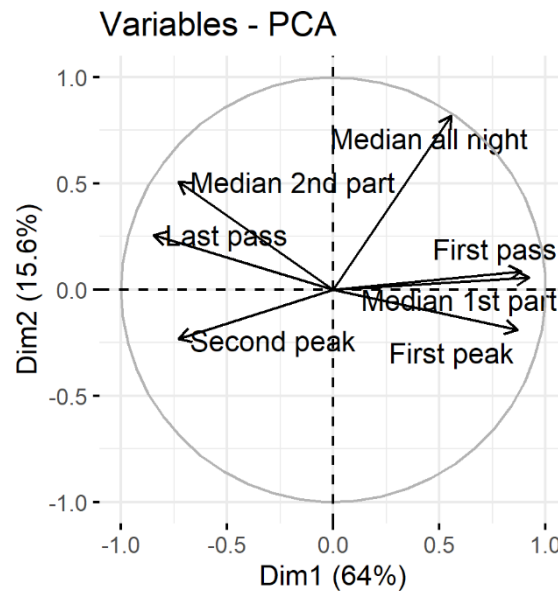


Fig. J.1: PCA graph of variables (R package *factoextra* (Kassambara and Mundt, 2020)).
The two first dimension explain 79.6% if the total inertia.

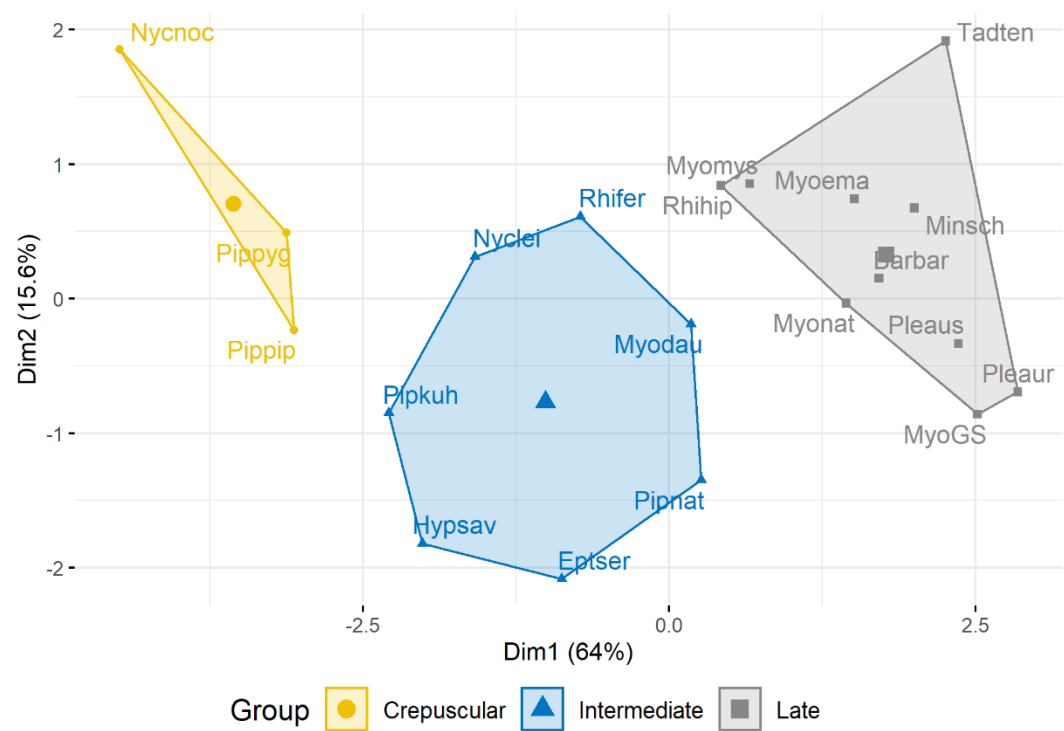


Fig. J.2: Visualisation of the clustering results: species (correspondence between the codes and the full Latin and English names in Table F) are represented by points in the plot, using principal components of the PCA. An ellipse is drawn around each cluster.

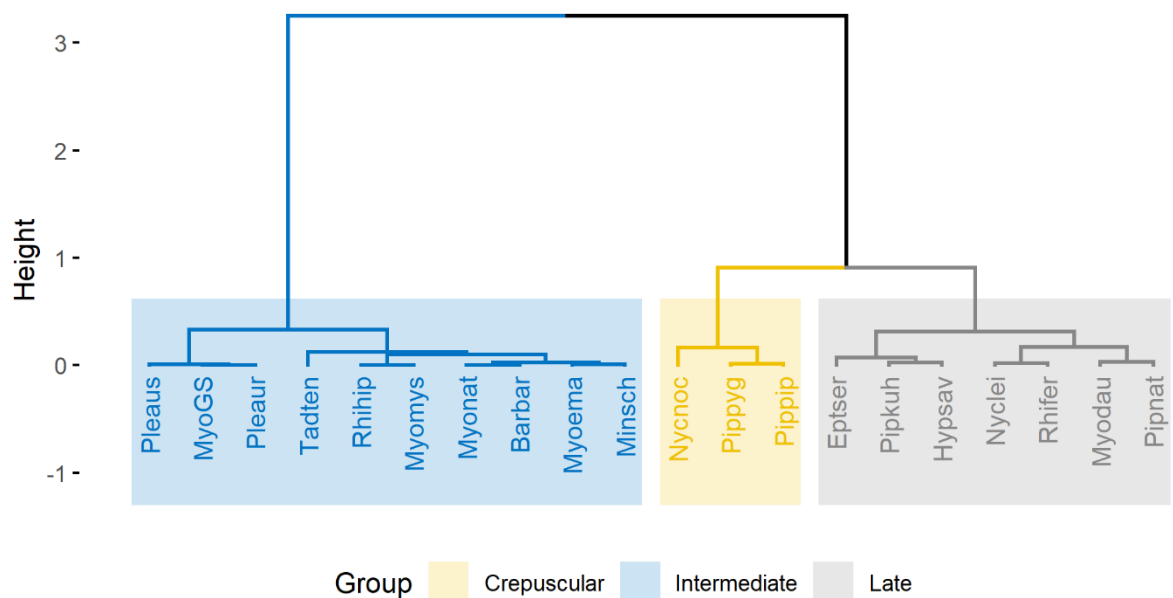


Fig J.3: Visualisation of the clustering results: cluster dendrogram (correspondence between the species codes and the full Latin and English names in Table F).

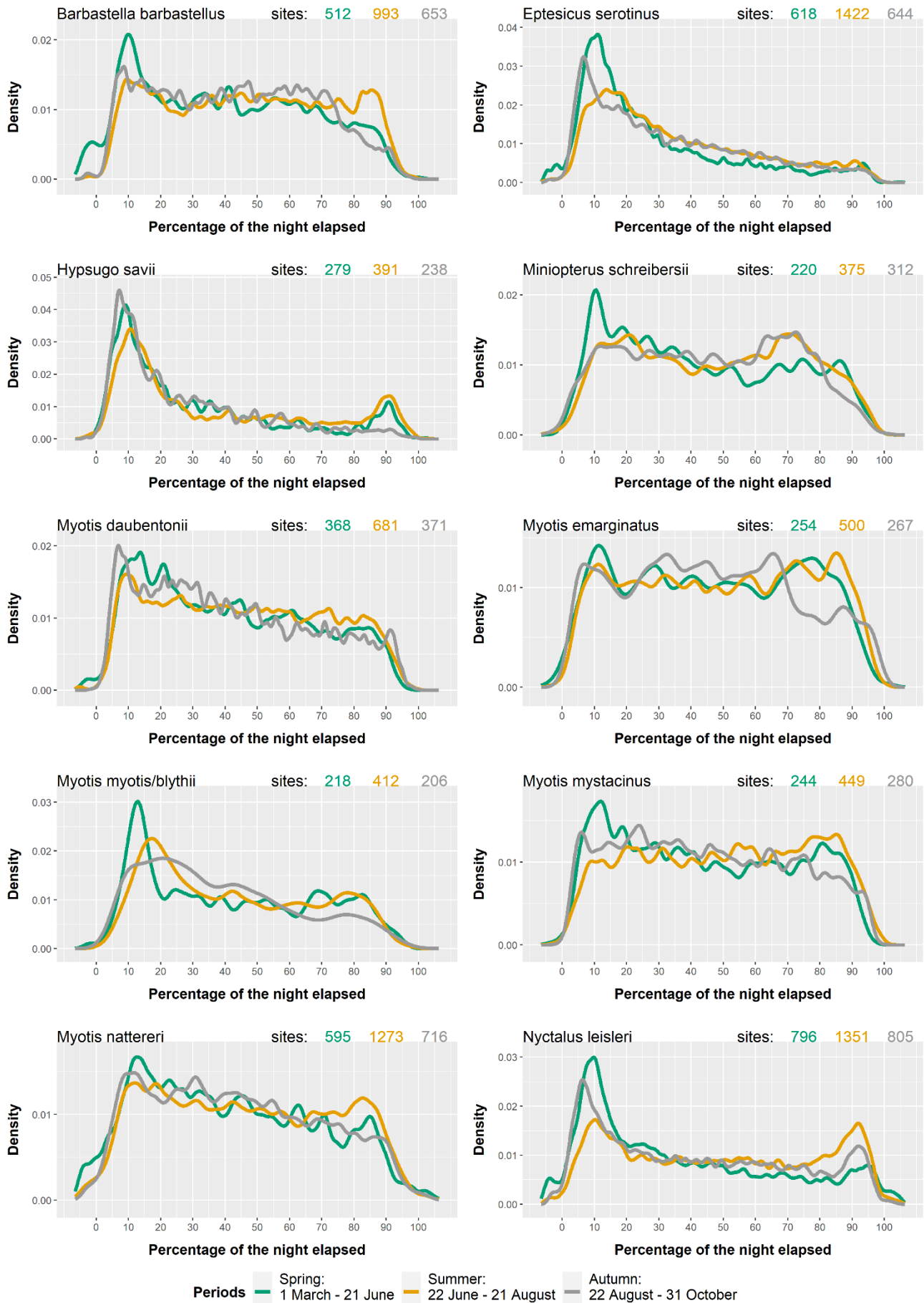
Table J.1: Description of the clusters: “*Average in cluster*” and “*Sd in cluster*” correspond respectively to the average and the standard deviation of the variables (mean times of the key descriptors or times of the activity peaks) for the species in the cluster, “*Overall average*” and “*Overall sd*” correspond respectively to the overall average and the standard deviation of the variables for all species. In the columns “*v.test*” and “*p.value*”, the following hypothesis was tested: “*the average of the cluster is equal to the overall average*”: the sign of the *v.test* indicates if the average of the cluster was greater or lower than the overall average and a value of the *v.test* > 1.96 corresponds to a *p-value* < 0.05. The “*Cluster*” column indicates according to which cluster the variable was considered (C: crepuscular species, I: intermediate species, L: late species). Only variables for which the *p-value* was lower than 0.05 for the cluster are shown.

Key descriptors	v.test	Average in cluster	Overall average	Sd in cluster	Overall sd	p.value	Cluster
TLast	3.1524	91.5432	83.7215	0.9669	4.5433	0.0016	C
TMedianP2	2.9308	78.2486	72.7010	4.6240	3.4660	0.0034	C
TPeakP2	2.0884	92.7357	85.8413	1.1736	6.0449	0.0368	C
TPeakP1	-2.5868	5.1786	9.6639	0.6504	3.1750	0.0097	C
TMedianP1	-2.6466	18.2917	23.3792	3.1399	3.5200	0.0081	C
TFirst	-2.6873	4.8600	12.1035	1.8755	4.9356	0.0072	C
TMedian	-2.6583	36.9832	41.6701	5.3433	5.6393	0.0079	I
TFirst	-2.6598	36.9832	41.6724	5.3433	5.6390	0.0078	L
TMedianP1	3.3827	15.9338	12.1035	2.7818	4.9356	0.0007	L
TPeakP1	3.2153	25.9757	23.3792	1.4885	3.5200	0.0013	L
TMedian	3.1553	11.9622	9.6639	2.4694	3.1750	0.0016	L
TLast	3.0422	45.6081	41.6724	3.1213	5.6390	0.0023	L
TPeakP2	-2.8332	80.7684	83.7215	2.9510	4.5433	0.0046	L

Bibliography:

- Husson, F., Josse, J., Pagès, J., 2010. Principal component methods-hierarchical clustering-partitional clustering: why would we need to choose for visualizing data? (Technical Report of the Applied Mathematics Department). Agrocampus.
- Kassambara, A., Mundt, F., 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses.

Appendices – Appendix I



Appendices – Appendix I

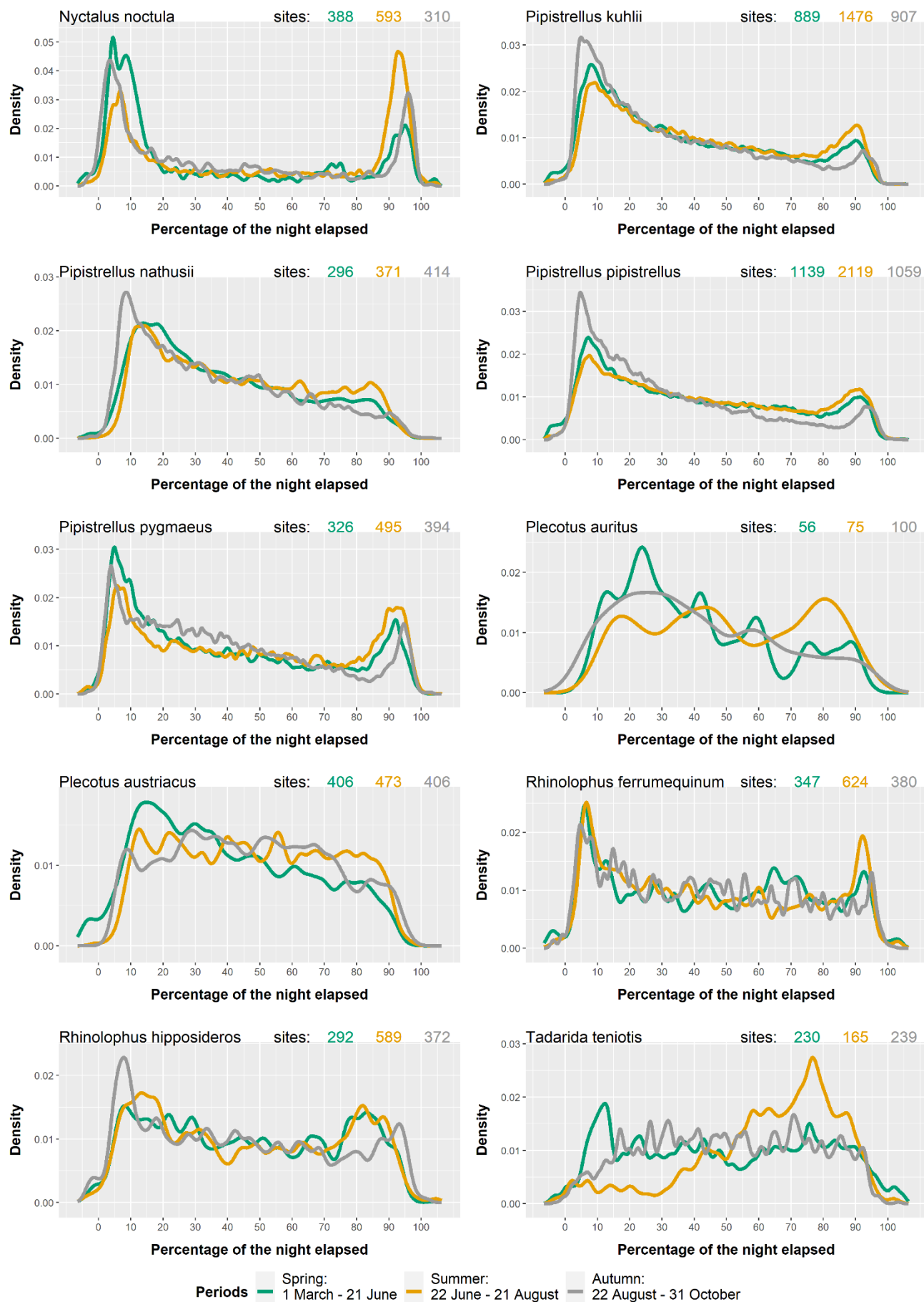


Fig. K: Activity distribution throughout the night for the 20 species studied according to season, in percentage of the night elapsed. Top right, number of sites considered for each season.

Appendix II: Online appendices of Mariton et al. (2022)

Supplementary material A: Consistency of the results obtained for datasets built with a maximum error rate tolerance of 0.5 with datasets built with a maximum error rate tolerance of 0.1

1. Relative abundance

The best model obtained with the dredge (i.e. the one with the lowest AICc – second order bias correction for Akaike information criterion) was the following one:

$$\begin{aligned} \text{Relative abundance metric} \sim & \text{Conifer_forest} + \text{Deciduous_forest} + \text{Julian_day} + \text{Moonlight} + \\ & \text{Small_woody_features} + \text{Habitat_diversity} + \text{ALAN} + \text{Cloud_cover} + \\ & \text{Difference_precipitations} + \text{Difference_temperature} + \text{Temperature} + \text{Latitude} + \\ & \text{Recorder_type} + (1 \mid \text{site} / \text{participation}) \end{aligned} \quad \text{Eq. (A.1)}$$

In Table A.1, we can see that the results were highly consistent whether the maximum error rate tolerance (MERT) chosen was 0.5 or 0.1. The variables which were significant in the best model with the 0.5 MERT remained significant with the 0.1 MERT, estimates that were negative remained negative and estimates that were positive remained positive.

Table A.1: Best model estimates and p-values (Anova II) for the “relative abundance” dataset with a MERT of 0.5 and 0.1. Latitude and recorder type are not represented as they were fixed terms in the dredge. All quantitative fixed effects were scaled.

MERT	0.5		0.1	
	Estimate	p-value	Estimate	p-value
Conifer_forest	0.3523	9.776e-06 ***	0.5109	1.048e-07 ***
Deciduous_forest	0.2659	0.0001009 ***	0.2725	0.0007871 ***
Julian_day	0.3330	2.792e-08 ***	0.4641	7.438e-10 ***
Moonlight	-0.1641	0.0019158 **	-0.2748	1.486e-05 ***
Small_woody_features	0.1945	0.0050122 **	0.1867	0.0261389 *
Habitat_diversity	0.1938	0.0109567 *	0.3240	0.0004355 ***
ALAN	-0.4374	1.481e-06 ***	-0.6077	1.476e-07 ***
Cloud_cover	0.0719	0.1155775	0.0004	0.9943969
Difference_precipitations	-0.1643	0.0006891 ***	-0.2604	1.457e-05 ***
Difference_temperature	0.3077	5.430e-07 ***	0.3816	8.046e-08 ***
Temperature	0.2659	8.719e-05 ***	0.2289	0.0045416 **

2. Timing of activity

The best model obtained with the dredge (i.e., the one with the lowest AICc) was the following one:

$$\begin{aligned}
 \text{Timing of activity metric} \sim & \text{Julian_day} + \text{Julian_day}^2 + \text{Moonlight} + \text{ALAN} + \text{Cloud_cover} + \\
 & \text{Difference_precipitations} + \text{Difference_temperature} + \text{Wind_speed} + \\
 & \text{Latitude} + \text{autocov} + \text{Moonlight} : \text{ALAN} + \text{ALAN} : \text{Cloud_cover} + (1 \mid \text{site})
 \end{aligned}
 \tag{A.2}$$

In Table A.2, we can see that, apart from ALAN, results were highly consistent whether the MERT chosen was 0.5 or 0.1. The variables which were significant in the best model with the 0.5 MERT remained significant with the 0.1 MERT, estimates that were negative remained negative and estimates that were positive remained positive.

Table A.2: Best model estimates and p-values (Anova II) for the “timing of activity” dataset with MERT of 0.5 and 0.1. Latitude and autocov are not represented as they were fixed terms in the dredge. All quantitative fixed effects were scaled.

MERT	0.5		0.9	
	Estimate	p-value	Estimate	p-value
Julian_day	-86.20	0.5302259	328.18	0.0884699 .
Julian_day²	354.78	0.0005707 ***	489.54	0.0008973 ***
Moonlight	291.01	0.0087162 **	334.29	5.815e-06 ***
ALAN	734.67	0.0001537 ***	-321.00	0.2231442
Cloud_cover	- 481.49	1.411e-12 ***	-410.73	1.852e-09 ***
Difference_precipitations	-164.92	0.0243367 *	-299.76	0.0027053 **
Difference_temperature	378.70	5.571e-08 ***	304.23	0.0006953 ***
Windspeed	-292.33	2.300e-05 ***	-306.21	0.0001368 ***
Moonlight : ALAN	-264.33	0.0016276 **	-1233.08	3.010e-08 ***
ALAN : Cloud_cover	178.24	0.0174029 *	457.85	0.0001788 ***

Despite being highly significant with a 0.5 MERT, ALAN became not significant with a 0.1 MERT. By choosing a low MERT, we only kept 11,513 *E. serotinus* passes instead of 22,998 with a 0.5 MERT (i.e., -50% of passes) (Table A.3). The calculation of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first 4 h 30 min of the night) may hence have been be less precise, and, as we only considered nights with at least 10 *E. serotinus* passes, it also led us to take into account less nights and sites. We may therefore have lost too much statistical power to detect any effect of ALAN.

To check it, we performed a power analysis to assess, with a 0.5 MERT, the minimum number of passes needed to detect an effect of ALAN on the timing of activity. To do so, we generated subsets of our dataset with a 0.5 MERT based on a selection of 1000 to 22,750 *E. serotinus* passes. For each number of passes, we generated 200 subsets, we removed nights with less than 10 passes and recalculated the time of the median pass for each night. Then, on each subset, we ran our best model to extract ALAN estimate and p-value (Anova II). Finally, we computed the percentage of the 200 models, for each number of passes, for which ALAN estimate was positive with a significant p-value. When more than 80% of ALAN estimates were positive with a significant p-value, we concluded that the statistical power was strong enough to detect an ALAN effect on the timing of activity. We draw this percentage according to the

number of *E. serotinus* passes in the dataset (Figure A.1). We concluded that a minimum of roughly 13,500 passes should be included in the analyses to detect an effect of ALAN on the timing of activity, thus explaining why it was not detected with a 0.1 MERT which strongly restricted the number of *E. serotinus* passes to analyse.

Table A.3: Number of sites, nights and sounds kept for a 0.5 and a 0.1 MERT for the “relative abundance” and the “timing of activity” datasets.

	MERT	Number of passes all night	Number of passes first half of night
Relative	0.5	21,452	/
abundance	0.1	10,117	/
Timing of	0.5	22,998	19,489
activity	0.1	11,513	9,901

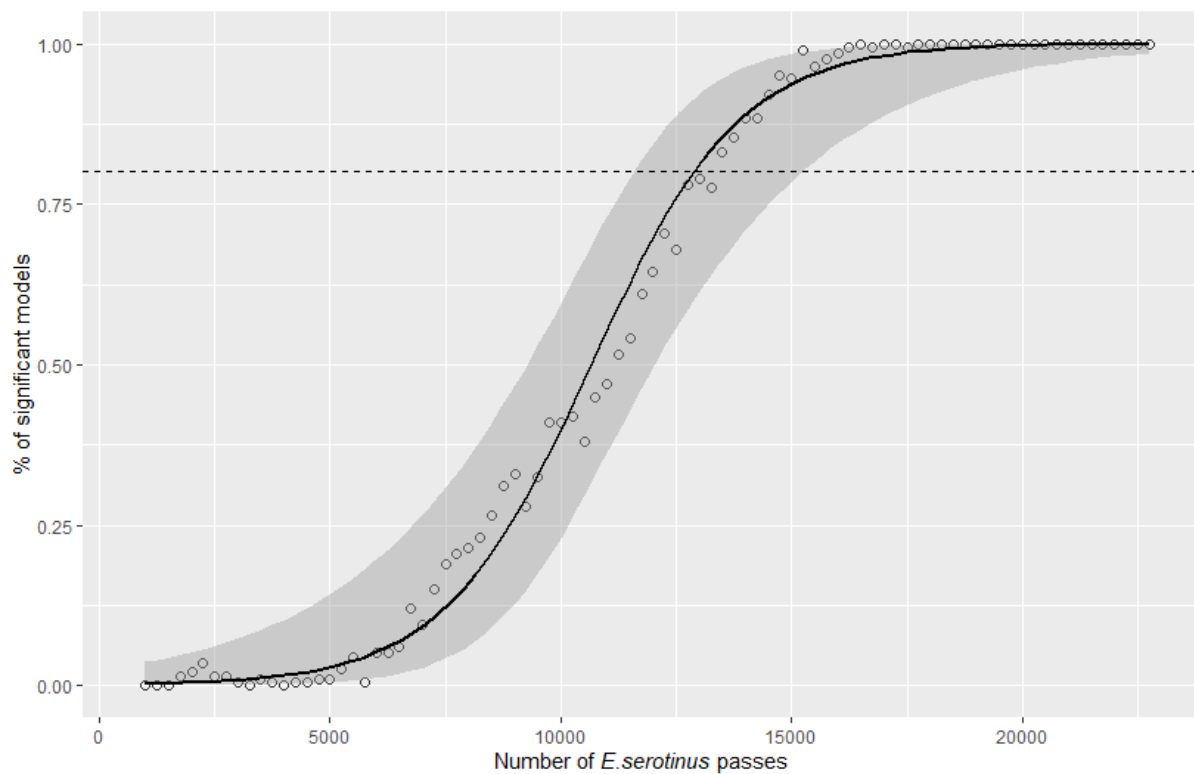


Figure A.1: Power analysis results: for each number of *E. serotinus* passes (from 1000 to 22,750), percentage of subsets that resulted in a positive and significant estimate for ALAN.

The dotted line represents the minimum 0.8 threshold below which the statistical power become insufficient. The solid curve represents the result of a binomial regression on the percentage of subsets that resulted in a positive and significant estimate for ALAN according to the number of *E. serotinus* passes.

Supplementary material B: Threshold on the number of *E. serotinus* passes for the “timing of activity” analyses

We postulated that no analysis of the timing of activity would be robust enough if there were not enough *E. serotinus* passes during the studied nights. Hence, we chose to only focus on nights with at least 10 *E. serotinus* passes. We then chose that the biological metric used to define the timing of activity would be the time of the median *E. serotinus* pass during the first half of the night (from 30 min before sunset to 4 h and 30 min after sunset).

We checked that the 10 passes threshold was a sensible choice by resampling the *E. serotinus* passes of the 100 nights with the most *E. serotinus* passes of our dataset (from 61 *E. serotinus* passes to 412). We followed procedure described in Figure B.1. and drew the Figure B.2. that synthesise the results obtained according to the number of passes considered. According to the generalised additive model (GAM) fitted to the data, for a 10 passes threshold, the predicted difference between the real median during the first half of the night and the calculated one would be of 5%, which made it a sensible threshold. For instance, the mean value of the median time for these 100 nights is 1 h 43 min 55 s, an incertitude of 5 % would hence be equal to 5 min 12 sec. Furthermore, we calculated the benefit in precision obtained when adding one more *E. serotinus* pass (Figure B.3.). According to the GAM fitted to the data, when using 11 *E. serotinus* passes instead of 10, we only had a benefit in precision of about 1.75% (for the mean time of the median – 1 h 43 min 55 s – of these 100 nights, it would correspond of a benefit in precision of 1 min 49 s) and this benefit kept on decreasing when the number of passes considered increased.

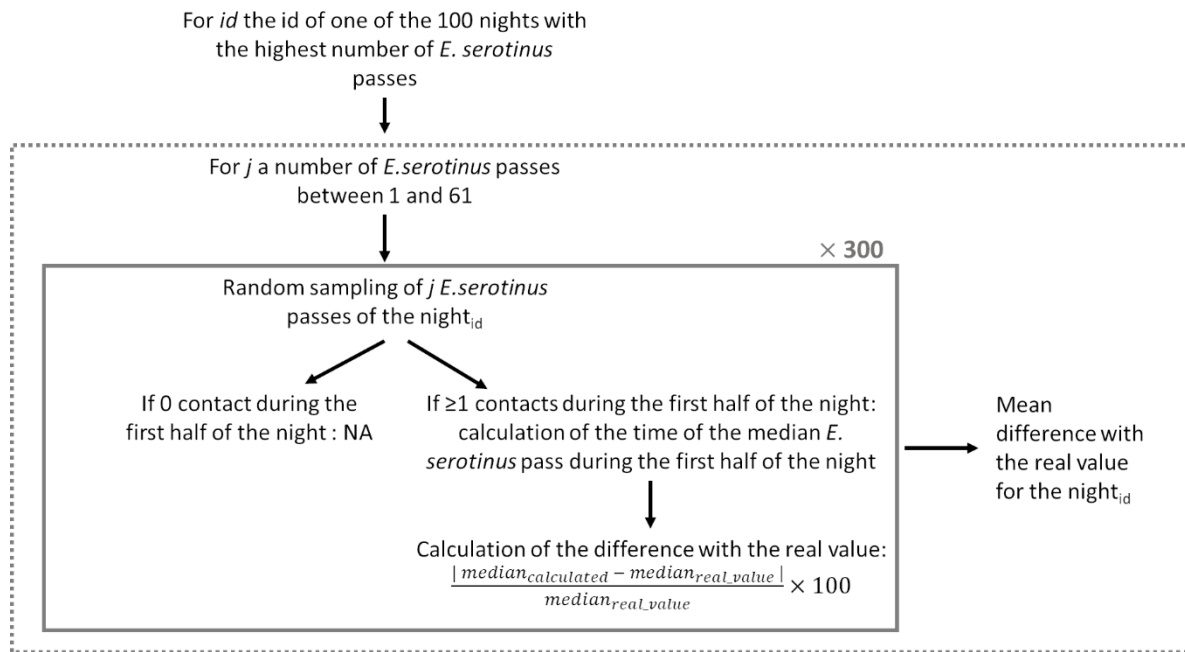


Figure B.1: Resampling procedure followed to check how many samples are needed for the timing of the median pass during the first half of the night to stabilize.

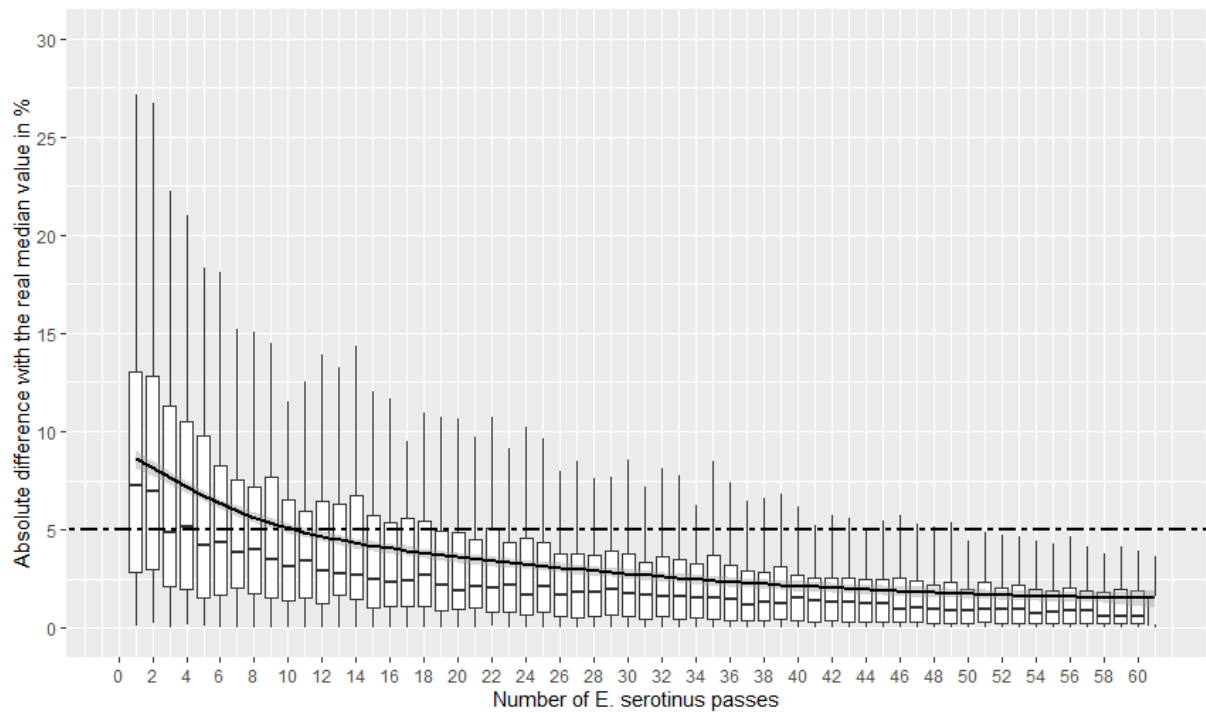


Figure B.2.: Boxplots synthesizing the mean difference between the known value of the median during the first half of the night and the calculated one after resampling according to a given number of *E. serotinus* passes 300 times (for the 100 nights with the highest number of *E. serotinus* passes). The solid curve represents the result of a GAM fitted to the data. The dashed line represents a 5% threshold for the absolute difference with the real median value.

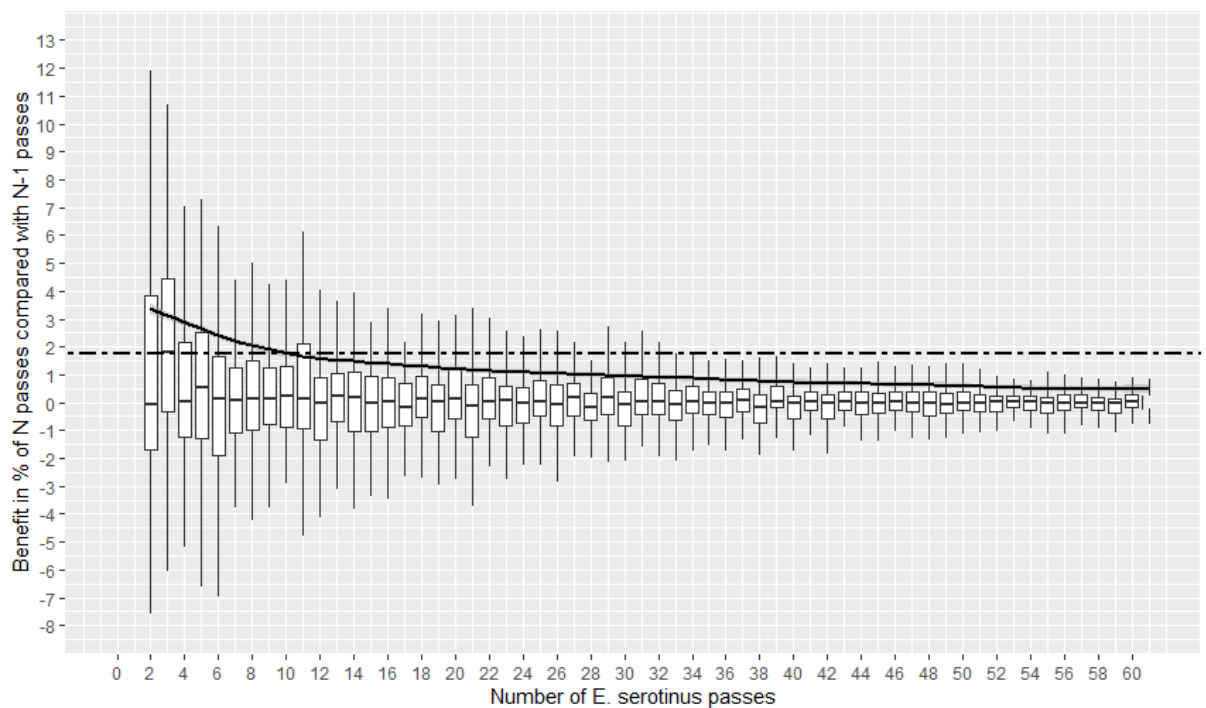


Figure B.3.: Boxplots synthesizing the benefit in precision obtained when adding one more *E. serotinus* pass. The solid curve represents the result of a GAM fitted to the data. The dashed line represents a benefit of 1.75% in precision when adding one more *E. serotinus* pass.

Supplementary material C: Comparison of the French radiance gradient with the radiance gradient in our datasets

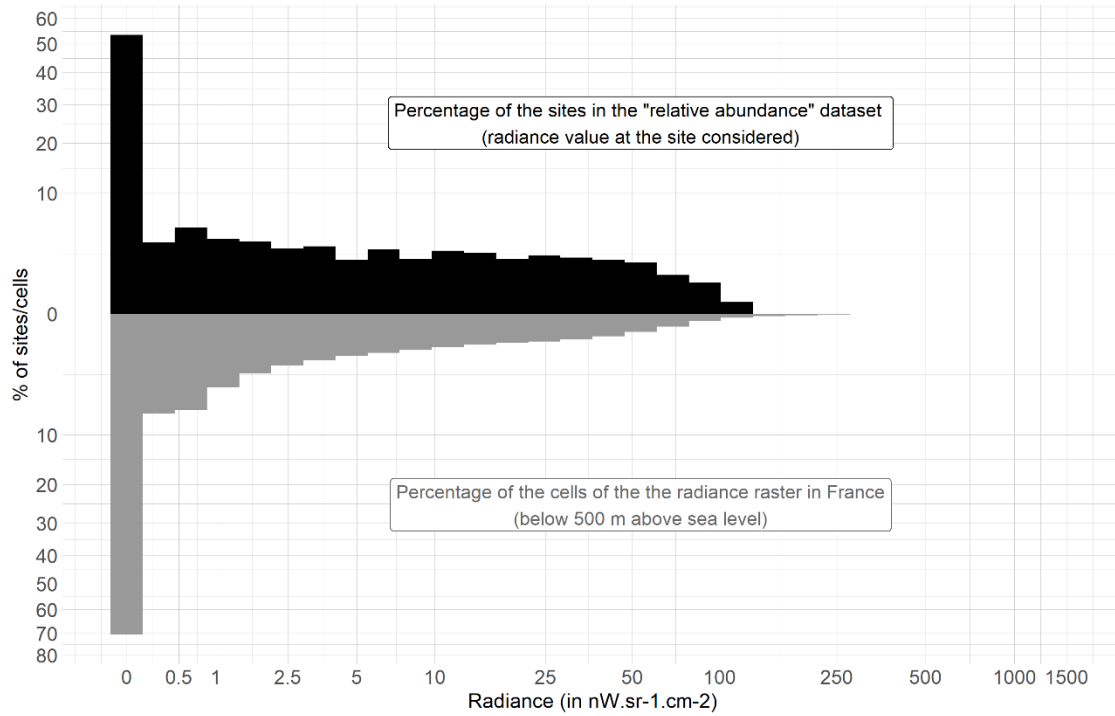


Figure C.1: Comparison of the French radiance gradient (radiance values of each raster cell of the VIIRS in France, which is below 500 m above sea level) with the radiance gradient of the studied sites in the “relative abundance” dataset (the radiance value considered is the radiance of the raster cell in which the site is located).

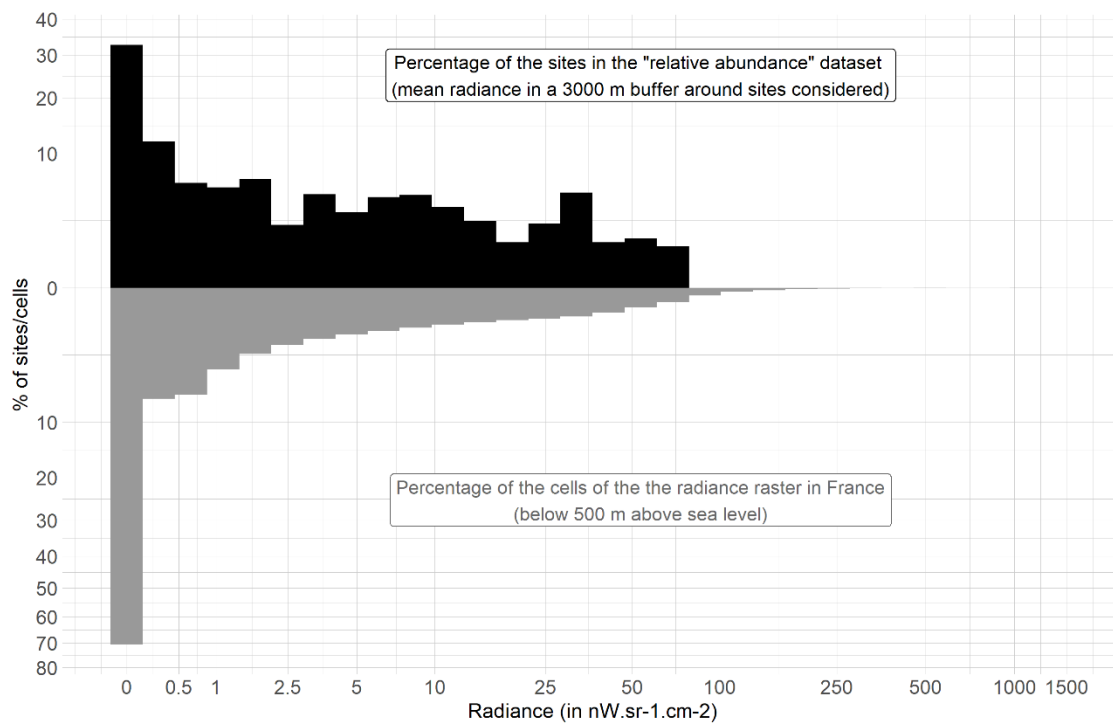


Figure C.2: Comparison of the French radiance gradient (radiance values of each cell of the VIIRS in France, which is below 500 m above sea level) with the radiance gradient of the studied sites in the “relative abundance” dataset (the radiance value considered is the mean radiance value across 3000 m buffer zones around sites).

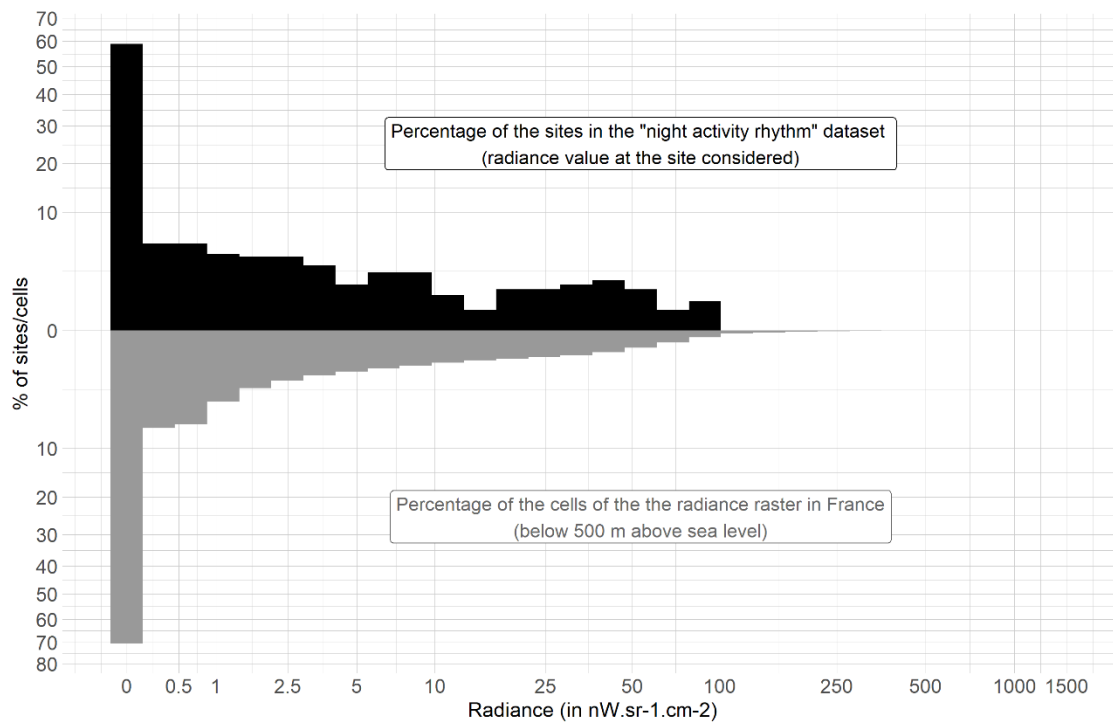


Figure C.3: Comparison of the French radiance gradient (radiance values of each cell of the VIIRS in France, which is below 500 m above sea level) with the radiance gradient of the studied sites in the “timing of activity” dataset (the radiance value considered is the radiance of the raster cell in which the site is located).

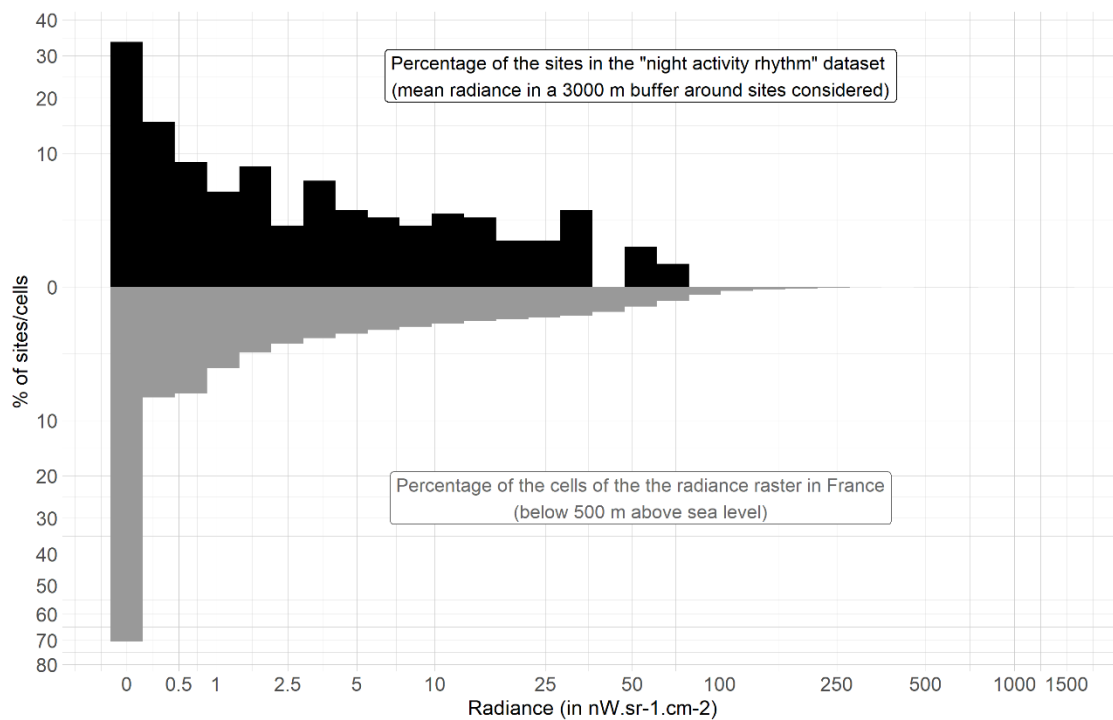


Figure C.4: Comparison of the French radiance gradient (radiance values of each cell of the VIIRS in France, which is below 500 m above sea level) with the radiance gradient of the studied sites in the “timing of activity” dataset (the radiance value considered is the mean radiance value across 3000 m buffer zones around sites).

Supplementary material D: Influence of the spatial scale at which the ALAN metric is calculated

1. Heterogeneity across 3000 m buffer zones

In this study, we hypothesised that bat spatiotemporal distribution might not only be impacted by light pollution levels at the recorder sites but more generally by light pollution at a larger spatial scale, similar to the scale of their vital domain. For example, if a roost is located in a light-polluted area, bats may emerge later from it and arrive later to their foraging sites whether they are light-polluted or dark. Such delay may then result in a reduced efficient time-budget to forage (i.e., a reduced time period during which bats may forage on the prey their diets are mainly composed of) with potential consequences on individual fitness, population dynamics and, *in fine*, bat abundance. Thus, we chose to focus on light pollution at landscape scale so that the metric would include light pollution within the whole *E. serotinus* vital domain and not only where the recordings were carried out. To do so, we considered buffer zones with a radius of 3000 m around sites, as it covered the mean distance between foraging sites and roosts (Catto et al., 1996; Kervyn, 2001; Robinson & Stebbings, 1997).

We measured radiance (i.e., ALAN) heterogeneity in the 3000 m buffer zones around sites by calculating standard deviations and coefficients of variation across them. The higher the mean radiance in the 3000 m buffer zones around sites, the higher was the standard deviation but the lower was the coefficient of variation in the buffer zones (see Table D.1 for a summary of these metrics for both dataset and Figure D.1 and D.2 for graphic representations).

Despite some heterogeneity in the buffer zones, the Pearson Correlation Coefficients (PCC) between the mean radiance in the 3000 m buffer zones around sites and the radiance at the sites were high (PCC = 0.87 for the “relative abundance” dataset and PCC = 0.86 for the “timing of activity” dataset). Such correlations suggested that generally, the radiance at the recorder sites was representative of the radiance in the buffer zones around sites.

Table D.1.: Number of raster cells, mean radiance, standard deviance and coefficient of variation in the 3000 m buffer zones around sites. The coefficient of variation is equal to 0 if the mean radiance and the standard deviation are equal to 0, to standard deviation divided by mean radiance otherwise.

	Number of cells	Mean radiance	Standard deviation	Coefficient of variation
Relative abundance dataset	mean: 229.2 (min:225; max: 232)	mean: 6.34 (min:0; max: 74.1)	mean: 4.7 (min:0; max: 36.7)	mean: 2.4 (min:0; max: 15.2)
Timing of activity dataset	mean: 229.3 (min:225; max: 232)	mean: 4.1 (min:0; max: 62.0)	mean: 3.8 (min:0; max: 24.4)	mean: 2.6 (min:0; max: 15.1)

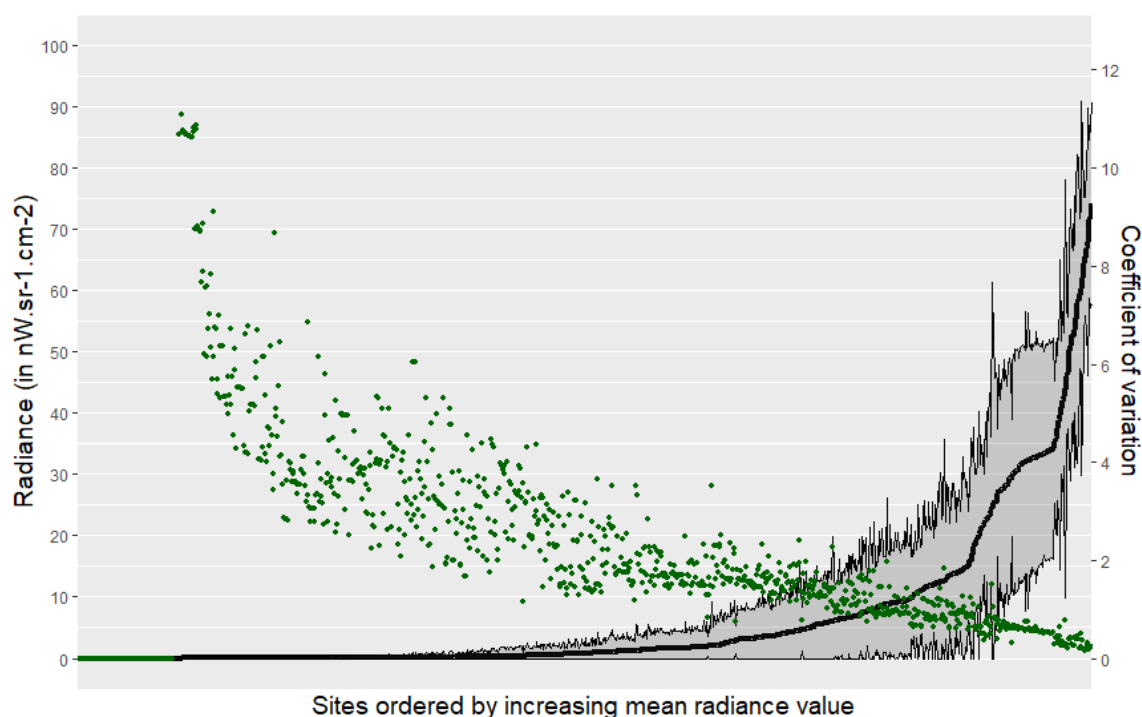


Figure D.1: Radiance variation in each 3000 m buffer zone for the “relative abundance” dataset. Sites are ordered by increasing mean radiance value, this value being represented by the solid line. The grey ribbon upper limit corresponds to the mean radiance value in the buffer zone plus the standard deviation in the buffer zone. The lower limit is equal to zero if the mean radiance is lower than the standard deviation, and to the mean radiance minus the standard deviation otherwise. The green dots represent the coefficient of variance of the radiance in each 3000 m buffer zone (equal to 0 if the mean radiance and the standard deviation in the buffer are equal to 0).

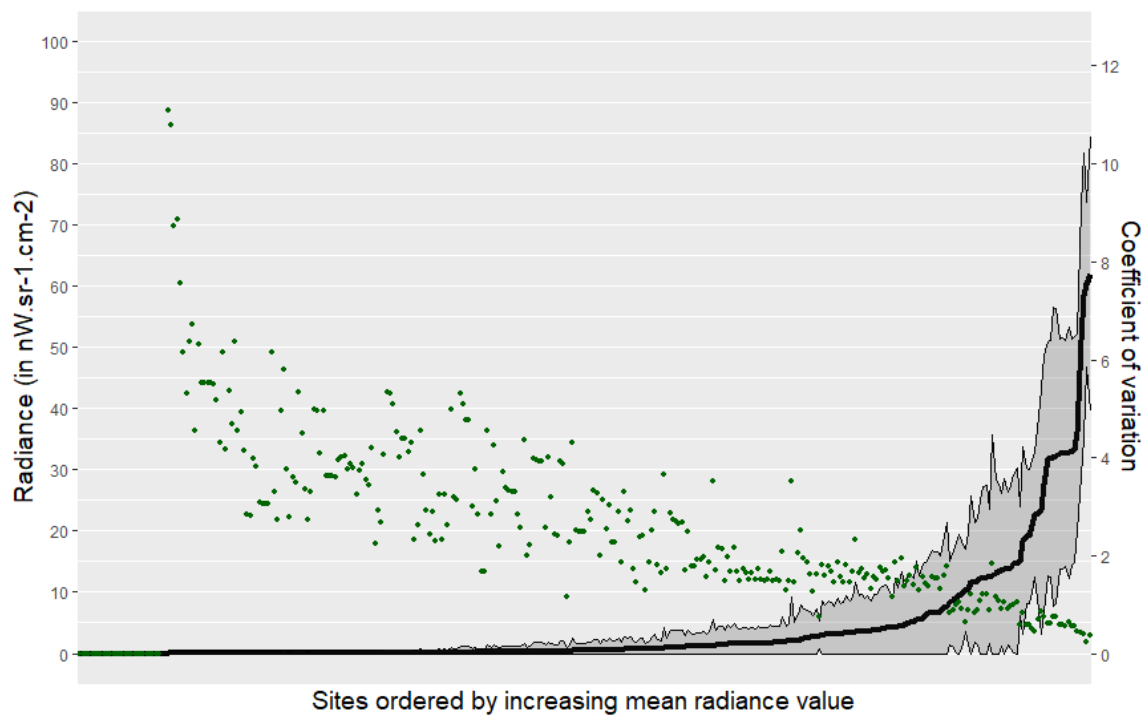


Figure D.2: ALAN variation in each 3000 m buffer zone for the “timing of activity” dataset. Sites are ordered by increasing mean radiance value, this value being represented by the solid line. The grey ribbon upper limit corresponds to the mean radiance value in the buffer zone plus the standard deviation in the buffer zone. The lower limit is equal to zero if the mean radiance is lower than the standard deviation, and to the mean radiance minus the standard deviation otherwise. The green dots represent the coefficient of variance of the radiance in each 3000 m buffer zone (equal to 0 if the mean radiance and the standard deviation within the buffer are equal to 0).

2. Analyses with the ALAN value at the recorder sites

We carried the same analyses as those presented in the main text, but with the ALAN value of the VIIRS raster cell ($\sim 351 \text{ m} \times 351 \text{ m}$) in which the sites were, instead of the mean ALAN value in 3000 m buffer zones around sites.

Interestingly for both the “relative abundance” and “timing of activity” analyses, the AICc (second order bias correction for Akaike Information Criterion) was lower when considering the mean ALAN value in buffer zones rather than the ALAN value at the sites (Table D.2). For the “relative abundance” analyses, the results with the ALAN value at the sites were quite similar to those obtained with the mean ALAN value in the buffer zones, the same

estimates had a 95% confidence interval that did not overlap zero (Table D.3). However, with the ALAN value at the sites, artificialized surfaces had a much higher sum of weights ($SW = 0.87$) than ALAN ($SW = 0.13$). For the “timing of activity” analyses, the results with the ALAN value at the sites were quite similar to those obtained with the mean ALAN value in the buffer zones, the same estimates had a 95% confidence interval that did not overlap zero, apart from the interactions (Table D.4). As a matter of fact, when considering the ALAN value at the site, the estimates of the interactions between ALAN and moonlight, and ALAN and cloud cover overlapped zero.

Table D.2: Results of the model averaging for the “relative abundance” and the “timing of activity” analyses. Even if a lot of models were selected in these analyses, the differences between the AICc of the null model and the AICc of the best model were always high.

		Number of models in a $\Delta AICc$ of 6	AICc of the best model	AICc of the null model	AICc null model* – AICc best model
Relative abundance dataset	ALAN site	128	10,545	10,796	251
	ALAN buffer	373	10,542	10,796	254
Timing of activity dataset	ALAN site	350	27,844	27,991	147
	ALAN buffer	142	27,831	27,991	160

*include the random effects for “relative abundance” and “timing of activity” analyses, include the weight on the logarithm of the number of *E. serotinus* passes for the “timing of activity” analyses.

Table D.3: Model averaging results for a delta AICc of six points for the “relative abundance” analyses: estimate, sum of weights (SW) and 95% confidence interval (CI) for each variable (apart from latitude and recorder type that were fixed) (estimates in bold when the 95% confidence interval did not overlap zero and the SW was above 0.60). Results with the ALAN value at the recorder sites as the ALAN metric and with the mean ALAN value in the 3000 m buffer zones as the ALAN metric are both represented so that they might be compared. All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable.

	With the ALAN value at the sites as the ALAN metric			With mean ALAN value in the 3000 m buffer zones as the ALAN metric		
Variables	Estimates	SW	CI (95%)	Estimates	SW	CI (95%)
Temperature	0.0100	1.00	0.005 ; 0.015	0.0098	1.00	0.0047 ; 0.0150
Difference_temperature	0.0110	1.00	0.007 ; 0.016	0.0118	1.00	0.0071 ; 0.0164
Windspeed	-0.0020	0.46	-0.006 ; 0.001	-0.0025	0.47	-0.0060 ; 0.0011
Difference_precipitations	-0.0060	1.00	-0.010 ; -0.003	-0.0061	1.00	-0.0098 ; -0.0024
Julian_Day	0.0120	1.00	0.008 ; 0.017	0.0124	1.00	0.0077 ; 0.0171
(Julian_Day) ²	-0.0020	0.32	-0.007 ; 0.003	-0.0023	0.32	-0.0072 ; 0.0027
Cloud_cover	0.0030	0.68	-0.001 ; 0.006	0.0026	0.67	-0.0009 ; 0.0061
Artificialized_surfaces	-0.0160	0.87	-0.023 ; -0.009	-0.0156	0.11	-0.0227 ; -0.0086
Grassland	-0.0040	0.37	-0.010 ; 0.003	-0.0047	0.50	-0.0114 ; 0.0020
Deciduous_forest	0.0100	1.00	0.005 ; 0.016	0.0096	1.00	0.0041 ; 0.0151
Conifer_forest	0.0130	1.00	0.007 ; 0.020	0.0124	1.00	0.0057 ; 0.0192
Habitat_diversity	0.0090	1.00	0.003 ; 0.015	0.0068	0.82	0.0005 ; 0.0132
Min_distance_freshwater	-0.0030	0.31	-0.010 ; 0.004	-0.0039	0.37	-0.0116 ; 0.0037
Small_woody_features	0.0090	1.00	0.003 ; 0.014	0.0082	1.00	0.0026 ; 0.0138
ALAN	-0.0140	0.13	-0.020 ; -0.007	-0.0186	0.89	-0.0268 ; -0.0104
Moonlight	-0.0060	1.00	-0.010 ; -0.002	-0.0065	1.00	-0.0105 ; -0.0025
Difference_temperature:Temperature	0.0010	0.27	-0.003 ; 0.005	0.0009	0.24	-0.0026 ; 0.0045
Cloud_cover:Moonlight	0.0020	0.23	-0.002 ; 0.005	0.0015	0.21	-0.0017 ; 0.0047
ALAN:Cloud_cover	0.0010	0.01	-0.004 ; 0.005	-0.0011	0.14	-0.0056 ; 0.0035
Moonlight:ALAN	0.0000	0.01	-0.004 ; 0.005	-0.0006	0.19	-0.0048 ; 0.0036

Table D.4: Model averaging results for a delta AICc of six points for the “timing of activity” analyses: estimate, sum of weights (SW) and 95% confidence interval (CI) for each variable (apart from latitude and the autocovariate that were fixed) (estimates in bold when the 95% confidence interval did not overlap zero and the SW was above 0.60). Results with the ALAN value at the recorder sites as the ALAN metric and with the mean ALAN value in the 3000 m buffer zones as the ALAN metric are both represented so that they might be compared. All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable.

	With the ALAN value at the sites as the ALAN metric			With mean ALAN value in the 3000 m buffer zones as the ALAN metric		
Variables	Estimates	SW	CI (95%)	Estimates	SW	CI (95%)
Temperature	0.034	0.28	-0.044 ; 0.112	0.031	0.31	-0.047 ; 0.110
Difference_temperature	0.113	1.00	0.062 ; 0.164	0.114	1.00	0.064 ; 0.165
Windspeed	-0.092	1.00	-0.135 ; -0.048	-0.093	1.00	-0.136 ; -0.050
Difference_precipitations	-0.051	0.89	-0.097 ; -0.004	-0.053	0.91	-0.099 ; -0.006
Julian_Day	-0.013	1.00	-0.099 ; 0.074	-0.031	1.00	-0.119 ; 0.057
(Julian_Day) ²	0.152	1.00	0.074 ; 0.231	0.142	1.00	0.061 ; 0.223
Cloud_cover	-0.157	1.00	-0.201 ; -0.113	-0.155	1.00	-0.199 ; -0.110
Artificialized_surfaces	0.169	0.12	0.053 ; 0.285	NA	NA	NA
Grassland	-0.019	0.16	-0.132 ; 0.095	0.012	0.18	-0.111 ; 0.135
Deciduous_forest	-0.077	0.31	-0.205 ; 0.052	-0.059	0.26	-0.189 ; 0.072
Conifer_forest	-0.026	0.18	-0.144 ; 0.092	-0.017	0.18	-0.138 ; 0.104
Habitat_diversity	0.020	0.18	-0.087 ; 0.127	0.017	0.18	-0.090 ; 0.123
Min_distance_freshwater	0.027	0.17	-0.121 ; 0.176	0.041	0.20	-0.107 ; 0.190
Small_woody_features	-0.044	0.25	-0.157 ; 0.068	-0.067	0.36	-0.181 ; 0.047
ALAN	0.167	0.88	0.060 ; 0.273	0.235	1.00	0.117 ; 0.354
Moonlight	0.076	0.99	0.016 ; 0.135	0.092	1.00	0.032 ; 0.152
Difference_temperature:Temperature	-0.011	0.04	-0.053 ; 0.031	-0.024	0.09	-0.066 ; 0.019
Cloud_cover:Moonlight	-0.007	0.17	-0.050 ; 0.035	-0.013	0.21	-0.055 ; 0.030
ALAN:Cloud_cover	-0.004	0.14	-0.053 ; 0.046	0.059	0.95	0.011 ; 0.106
Moonlight:ALAN	-0.044	0.39	-0.107 ; 0.020	-0.073	1.00	-0.12 ; -0.027

In the “relative abundance” analyses, the selection of artificialized surfaces over ALAN when considering ALAN value at local scale might be explained by several mechanisms. First, Azam et al. (2016) showed that *E. serotinus* abundance at landscape scale was negatively impacted by light pollution. However, locally, *E. serotinus* can forage near streetlight to benefit from the high densities of insect they attract (Stone et al., 2015) but at a slighter higher scale (from 25 to 50 m from streetlights) an avoidance behaviour might be observed (Azam et al., 2018). Hence, we hypothesised that ALAN would reduce *E. serotinus* abundance at landscape scale but we did not have strong hypotheses on what would be the local effect of light pollution on abundance. Furthermore, the mean ALAN value in the 3000 m buffer zones around sites was highly correlated to the ALAN value at the sites (PCC = 0.87 for the “relative abundance” dataset) but also to the percentage of artificialized surfaces in the 3000 m buffer zones (PCC = 0.88). Hence, the artificialized surfaces effect might also reflect the ALAN effect at landscape scale.

In the “timing of activity” analyses, we did not find any effect of the interactions between ALAN and moonlight, and ALAN and cloud cover when we considered the ALAN value at the recording sites. These two interactions were put in the model to evaluate how diffuse light pollution might interact with other environmental factors. Hence, it is not surprising that, when considering light pollution locally, these interactions did not have any effect any more. Moonlight affect the whole landscape (i.e., the whole *E. serotinus* vital domain) and thus, its effect might be weaker if globally there is a high light pollution intensity. Likewise, cloud cover might amplify diffuse light pollution at landscape scale whereas it should not have any effect on the local light pollution level directly created by several localised streetlights.

Bibliography

Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., & Kerbiriou, C. (2018).

Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning*, 175, 123–135.

<https://doi.org/10.1016/j.landurbplan.2018.02.011>

Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., & Kerbiriou, C. (2016). Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecology*, 31(10), 2471–2483.

<https://doi.org/10.1007/s10980-016-0417-3>

- Catto, C. M. C., Hutson, A. M., Racey, P. A., & Stephenson, P. J. (1996). Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology*, 238(4), 623–633. <https://doi.org/10.1111/j.1469-7998.1996.tb05419.x>
- Kervyn, T. (2001). *Ecology and ethology of the serotine bat, Eptesicus serotinus (Chiroptera, Vespertilionidae): Perspectives for the conservation of bats*. University of Liège.
- Robinson, M. F., & Stebbings, R. E. (1997). Activity of the serotine bat, *Eptesicus serotinus*. *Myotis*, 35, 5–16.
- Stone, E. L., Harris, S., & Jones, G. (2015). Impacts of artificial lighting on bats: A review of challenges and solutions. *Mammalian Biology*, 80(3), 213–219. <https://doi.org/10.1016/j.mambio.2015.02.004>

Supplementary material E: Details the calculation and selection of environmental variables

1. Moonlight

We included moonlight by extracting moon illumination at 9 PM (in %) (R package, *lunar*) and moonrise (R package *suncalc*) for each surveyed night. We then computed the following synthesis variable:

$$Moonlight = Moon_illumination \times Moonrise_bin \quad \text{Eq. (E.1)}$$

With:

Moon_illumination: moon illumination (in %) at 9 PM the day when the surveyed night began

Moonrise_bin: equal to zero if moonrise happened after the first 4 h and 30 min after sunset, equal to 1 if moonrise happened before or during the first 4 h and 30 min hours after sunset.

2. Weather

2.1. Calculation of the difference of weather with previous days

The difference of weather with previous days was defined as followed:

$$Weather_Diff_{Day\ n} = Weather_{Day\ n} - \left(\sum_{i=1}^5 Weather_{Day\ n-i} \times (6-i) \right) / 15 \quad \text{Eq. (E.2)}$$

With:

Weather: Temperature (anomaly), precipitations or windspeed

Day n: Day during which the night began

2.2. Calculation of the temperature and precipitation metrics

To extract temperature (in °C) and precipitation (in mm) data, we used the EObs daily gridded observational dataset for its high temporal (daily data) and spatial resolution (0.1 deg) (Copernicus, https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php#datafiles, Cornes et al., 2018) (R package *ncdf4*). Each studied site was associated to the grid cell whose centre was closer, and for each night the mean temperature and the sum of precipitations of the day when the night began were extracted.

Absolute measures of temperature may be misleading if *E. serotinus* populations adapt to local climatic conditions: a given temperature may represent a mild day for one population but a cold day for another. We therefore chose to transform temperature in temperature anomalies, defined as followed:

$$Anomaly_{YYYY/MM/DD} = Temperature_{YYYY/MM/DD} - \left(\sum_{i=1980}^{2010} Temperature_{i/MM/DD} \right) / 30 \quad \text{Eq. (E.3)}$$

With: *YYYY/MM/DD*: Day during which the surveyed night began (Year: *YYYY*, Month: *MM*, Day: *DD*)

2.3. Calculation of windspeed

For windspeed data, we used R package *RNCEP* (Kemp et al., 2012) to extract data from the NCEP/NCAR Reanalysis dataset (Kalnay et al., 1996). Data spatial resolution was 2.5 deg and we associated each site to the grid cell whose centre was closer. Data temporal resolution was high (6 hours) and we chose to extract data at 6 PM the day when the night began. We extracted the U-Wind Component [East/West] (in m.s⁻¹) and the V-Wind Component [North/South] (in m.s⁻¹) and defined windspeed (in m.s⁻¹) as followed:

$$Wind_speed = \sqrt{(U_wind_component)^2 + (V_wind_component)^2} \quad \text{Eq. (E.4)}$$

2.4. Correlations

The precipitations of the day when the night began and the difference between the precipitations of the day when the night began and previous days (as defined in Eq. (B.2)) were correlated (Pearson Correlation Coefficient (PCC) = 0.62 for the “relative abundance” dataset and PCC = 0.56 for the “timing of activity” dataset), we therefore only kept the difference (it allowed to obtain a better AICc – second order bias correction for Akaike Information Criterion – when used in our full models for the timing of activity).

The windspeed of the day when the night began and the difference between the windspeed of the day when the night began and previous days (as defined in equation (2)) were highly correlated (PCC = 0.77 for the “relative abundance” dataset and PCC = 0.79 for the “timing of activity” dataset), thus we only kept windspeed of the day (it allowed to obtain a better AICc when used in our full models for the timing of activity).

2.5. Weather filter

To avoid exceptional weather conditions, we only selected nights with a windspeed below 12.5 m.s⁻¹ and a sum of precipitations below 20 mm on the day when the night began and the five previous days.

3. *Land-use*

3.1. Landscape representativity

The Vigie-Chiro program was originally design to study population trends for French bats. It should therefore be based on the representativeness of the sample design and, in particular, the representativeness of the habitat distribution in France. Thus, when a volunteer wanted to take part in the “stationary points protocol”, he was encouraged to survey sites that were randomly sampled near a municipality that he chose. However, if he wanted to, he could also choose where he wanted to carry out surveys.

Despite these precautions, the selection of sites might have been driven by unknown criteria, as the closeness to where the volunteers lived. To ensure that it was not an issue for our study, we compared the gradients of proportions of each land-use type in the 3000 m radius buffer zones around the monitored sites with what would have been found if the sites had strictly been randomly selected. To do so, we randomly sampled sites in a square grid (6000 m * 6000 m) in France and removed sites that were above 500 m above sea level (to fit with the altitude filter applied on our datasets). For each of the 12,252 randomly sampled sites, we calculated the proportion of each land-use type in 3000 m buffer zones and compared it with the proportion of each land-use type in the buffer zones around the studied sites of our datasets. Overall, the buffer zones around the sites of our datasets covered the same land-use type gradient as buffer zones around sites randomly selected in France. (Figure E.1).

3.2. Correlations

Even though road density could be a relevant variable (Claireau et al., 2019), it was not included in the analyses due to multi-collinearity issues: it was correlated with both artificialized surfaces (PCC = 0.68 for the “relative abundance” dataset and PCC = 0.63 for the “timing of activity” dataset) and ALAN (PCC = 0.59 for the “relative abundance” dataset and PCC = 0.50 for the “timing of activity” dataset).

Crops were the most frequent land-use type around sites and also led to multi-collinearity issues: it was correlated with conifer forest (PCC = - 0,66 for the “relative

abundance” dataset and $PCC = -0.73$ for the “timing of activity” dataset). As land-use impacts on bat abundance and timing of activity was not the focus of this study, we chose not to consider crops. However, we kept in mind that other habitat effects might reflect those of this land-use type.

ALAN and artificialized surfaces were highly correlated ($PCC = 0.88$ for the “relative abundance” dataset, $PCC = 0.83$ for the “timing of activity” dataset).

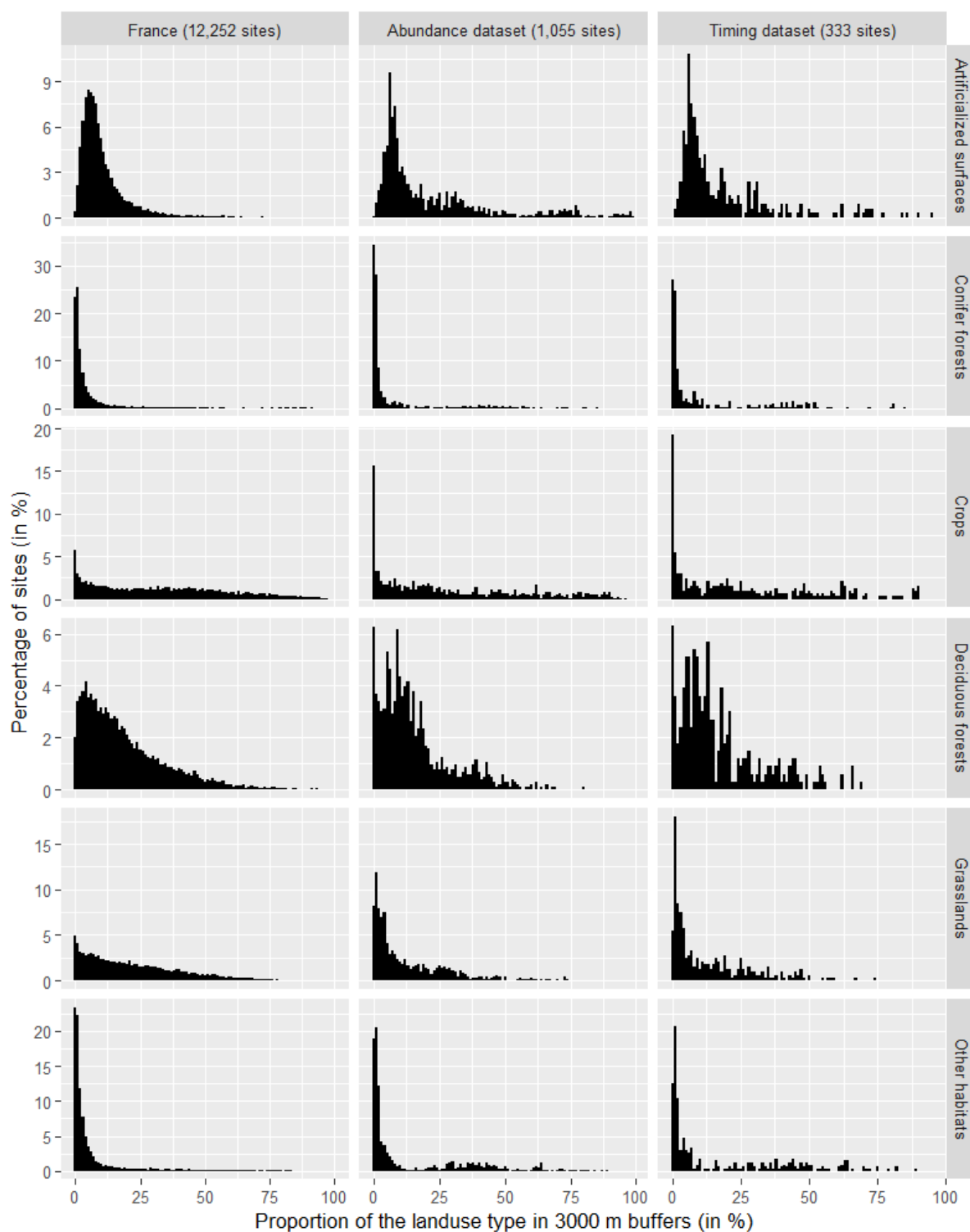


Fig E.1: Gradients of proportions of each land-use type in 3000 m buffer zones around randomly sampled sites in France (every 6000 m), the sites of the “relative abundance” dataset and the sites of the “timing of activity” dataset.

Bibliography

- Claireau, F., Bas, Y., Pauwels, J., Barré, K., Machon, N., Allegrini, B., Puechmaille, S. J., & Kerbiriou, C. (2019). Major roads have important negative effects on insectivorous bat activity. *Biological Conservation*, 235, 53–62.
<https://doi.org/10.1016/j.biocon.2019.04.002>
- Cornes, R. C., van der Schrier, G., van den Besselaar, E. J. M., & Jones, P. D. (2018). An Ensemble Version of the E-OBS Temperature and Precipitation Data Sets. *Journal of Geophysical Research: Atmospheres*, 123(17), 9391–9409.
<https://doi.org/10.1029/2017JD028200>
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, E., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., ... Joseph, D. (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, 77(3), 437–472.
- Kemp, M. U., Emiel van Loon, E., Shamoun-Baranes, J., & Bouten, W. (2012). RNCEP: Global weather and climate data at your fingertips: *RNCEP. Methods in Ecology and Evolution*, 3(1), 65–70. <https://doi.org/10.1111/j.2041-210X.2011.00138.x>

Supplementary material F: Gradient of cloud cover for the studied nights

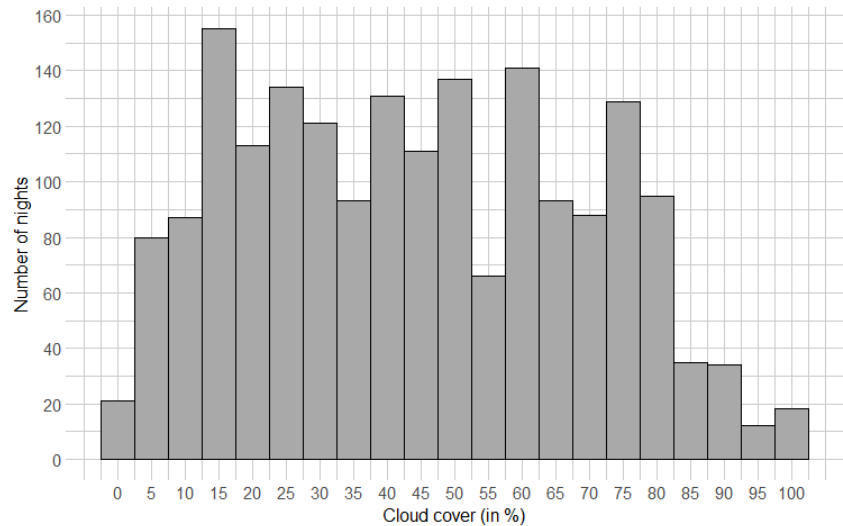


Figure F.1: Gradient of cloud cover (in %) for the studied nights of the “relative abundance” dataset.

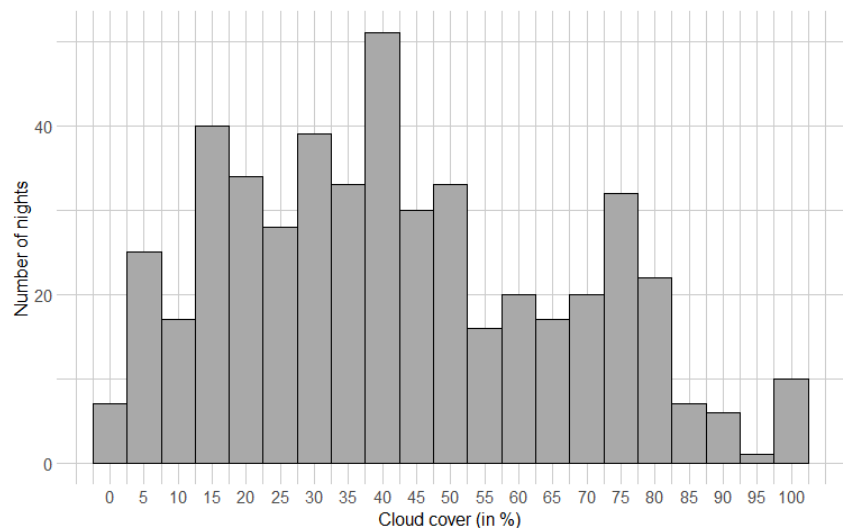


Figure F.2: Gradient of cloud cover (in %) for the studied nights of the “timing of activity” dataset.

Supplementary material G: Gradient of moonlight for the studied nights

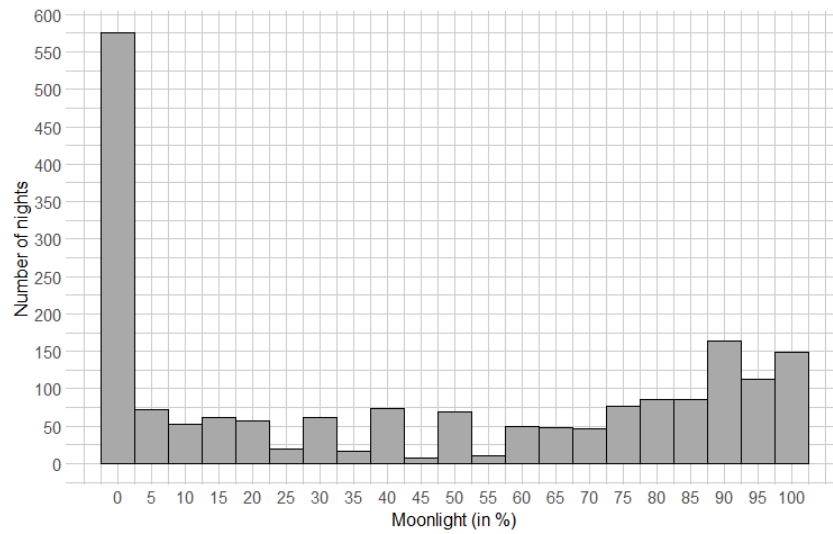


Figure G.1: Gradient of moonlight for the studied nights of the “relative abundance” dataset. The high number of zeros is explained by the construction of the metric, which was equal to moon illumination (in %) if moonrise happened before the first 4 h and 30 min after sunset during the studied night and zero otherwise.

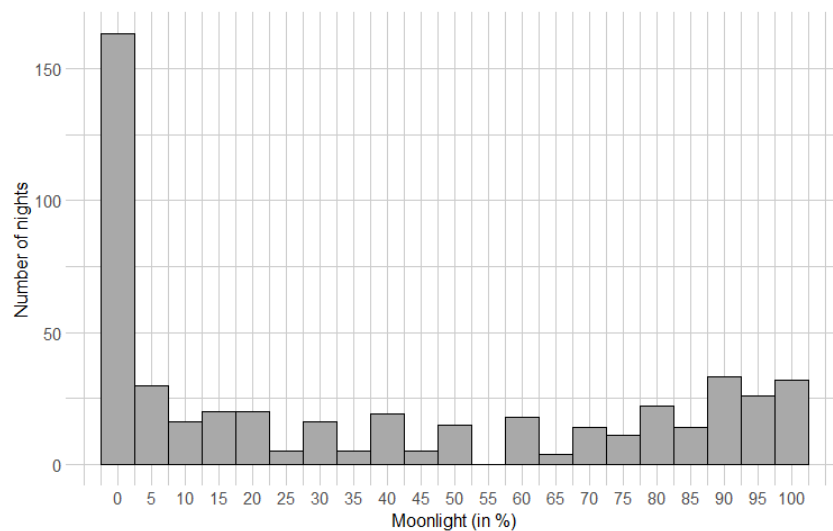


Figure G.2: Gradient of moonlight for the studied nights of the “timing of activity” dataset. The high number of zeros is explained by the construction of the metric, which was equal to moon illumination (in %) if moonrise happened before the first 4 h and 30 min after sunset during the studied night and zero otherwise.

Table H: Variables extracted to control exogenous factors that could impact *E. serotinus* relative abundance and timing of activity at their foraging site. The variables that have been discarded due to multi-collinearity issues are in brackets. Ab = “relative abundance” dataset, Ta = “timing of activity” dataset.

Variable	Mean (Min / Max)	Units	Description	References	Data source
Light pollution					
ALAN	<i>Ab</i> 0.55 (0.00 / 74.12) <i>Ta</i> 0.38 (0.00 / 62.98)	nW.sr ⁻¹ .cm ⁻²	Mean radiance	/	VIIRS DNB (a)
Environnemental data					
(Crops)	<i>Ab</i> 0.34 (0.00 / 0.96) <i>Ta</i> 0.30 (0.00 / 0.90)	%	Proportion of rape, cereal plant, protein, soya, sunflower and corn crops (3000 m buffer)	(Azam et al., 2016)	CESBIO ^(b)
Artificialized surfaces	<i>Ab</i> 0.22 (0.00 / 0.97) <i>Ta</i> 0.18 (0.01 / 0.93)	%	Proportion of dense and diffuse impervious surface, industrial and commercial estates (3000 m buffer)	(Azam et al., 2016)	CESBIO ^(b)
Conifer forest	<i>Ab</i> 0.06 (0.00 / 0.85) <i>Ta</i> 0.09 (0.00 / 0.85)	%	Proportion of conifer forest (3000 m buffer)	/	CESBIO ^(b)
Deciduous forest	<i>Ab</i> 0.14 (0.00 / 0.80) <i>Ta</i> 0.16 (0.00 / 0.69)	%	Proportion of deciduous forest (3000 buffer m)	(Boughey et al., 2011; Robinson & Stebbings, 1997b)	CESBIO ^(b)
Grasslands	<i>Ab</i> 0.13 (0.00 / 0.74) <i>Ta</i> 0.12 (0.00 / 0.74)	%	Proportion of grasslands (3000 m buffer)	(Boughey et al., 2011; Catto et al., 1996; Robinson & Stebbings, 1997b; Vaughan et al., 1997)	CESBIO ^(b)
(Road density)	<i>Ab</i> 2.30 (0.22 / 8.93)	km ⁻¹	Road density (3000 m buffer)	(Claireau et al., 2019)	ROUTE 500 ® ^(c)

Habitat diversity	<i>Ta</i> 2.07 (0.25 / 8.13)	/	Shannon's diversity index describing habitat diversity (R package <i>landscapemetrics</i>) (3000 m buffer)	/	CESBIO ^(b)
	<i>Ab</i> 1.74 (0.67 / 2.48)				
Small woody features density	<i>Ta</i> 1.74 (0.67 / 2.45)	km ⁻¹	Linear and patchy structures of trees, hedges, bushes and scrubs density (3000 m buffer)	(Lacoeuilhe et al., 2016; Verboom & Huitema, 1997)	Copernicus ^(d)
	<i>Ab</i> 0.04 (0.00 / 0.17)				
Minimum distance from freshwater	<i>Ta</i> 0.04 (0.00 / 0.16)	km	Minimum distance from lakes and watercourses	(Vaughan et al., 1997)	BD Carthage ^(e)
	<i>Ab</i> 945 (0 / 6404)				
	<i>Ta</i> 949 (0.00 / 4887)				
Meteorological and astronomical data					
Temperature anomaly	<i>Ab</i> 1.27 (-5.99 / 9.34)	°C	Mean temperature anomaly for the day when the night began	(Catto et al., 1995; Vaughan et al., 1997)	EObs ^(f)
	<i>Ta</i> 1.97 (-5.26 / 9.34)				
Difference temperature anomalies	<i>Ar</i> 0.48 (-7.74 / 7.25)	°C	Difference in anomalies between the day when the night began and the five previous days	(Catto et al., 1995)	EObs ^(f)
	<i>Ta</i> 1.20 (-4.99 / 7.25)				
Precipitations	<i>Ab</i> 1.29 (0.00 / 19.50)	mm	Sum of precipitations the day the night began	(Catto et al., 1996)	EObs ^(f)
	<i>Ta</i> 0.66 (0.00 / 12.8)				
Difference precipitations	<i>Ab</i> -0.40 (-12.30 / 19.32)	mm	Difference in precipitations between the day when the night began and the five previous days	/	EObs ^(f)
	<i>Ta</i> -0.67 (-8.90 / 12.28)				
Windspeed	<i>Ab</i> 5.50 (0.41 / 12.35)	m.s ⁻¹	Windspeed at 6 PM the day when the night began	(Catto et al., 1996)	NCEP/NCA R Reanalysis ^(g)
	<i>Ta</i> 5.38 (0.57 / 12.30)				
Difference windspeed	<i>Ab</i> -0.30 (-7.57 / 9.40)	m.s ⁻¹	Difference in wind speed between the	/	NCEP/NCA R

	<i>Ta</i> -0.40 (-7.57 / 9.40)		day when the night began and the five previous days		Reanalysis (g)
Cloud cover	<i>Ab</i> 44.23 (0.00 / 100) <i>Ta</i> 42.18 (0.00 / 100)	%	Cloud cover at 6 PM the day when the night began	(Kyba et al., 2015; McAney & Fairley, 1988)	NCEP/NCA R Reanalysis (g)
Moonlight	<i>Ab</i> 0.43 (0.00 / 1.00) <i>Ta</i> 0.37 (0.00 / 1.00)	%	Equal to 0 if no moon in the first 4 h 30 min after sunset, equal to moon illumination otherwise	(Appel et al., 2017; Kolkert et al., 2020; Lang et al., 2006)	R packages <i>suncalc</i> and <i>lunar</i>
Others					
Julian day	<i>Ab</i> 153 (121 / 171) <i>Ta</i> 155 (122 / 171)	/	Julian day of the day when the night began	(Catto et al., 1995; Robinson & Stebbins, 1997a)	/
Latitude	<i>Ab</i> 46.41 (41.92 / 50.65) <i>Ta</i> 46.37 (42.52 / 50.41)	°	Latitude of the monitored site	/	/
Recorder type	/	/	Type of recorder used	/	/

(a) EOG, <https://eogdata.mines.edu/products/vnl/>

(b) OSO, <http://osr-cesbio.ups-tlse.fr/oso/>

(c) IGN, <https://geoservices.ign.fr/documentation/diffusion/telechargement-donnees-libres.html#route-500>

(d) Copernicus, <https://land.copernicus.eu/pan-european/high-resolution-layers/small-woody-features/small-woody-features-2015>

(e) IGN, <https://geo.data.gouv.fr/fr/datasets/fa9cd96748649d68b59c2a65ebe78258dec4ceeb>

(f) Copernicus, https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php#datafiles

(g) Kalnay et al., 1996, extracted with R package *RNCEP* (Kemp et al., 2012)

Bibliography

- Appel, G., López-Baucells, A., Magnusson, W. E., & Bobrowiec, P. E. D. (2017). Aerial insectivorous bat activity in relation to moonlight intensity. *Mammalian Biology*, 85, 37–46. <https://doi.org/10.1016/j.mambio.2016.11.005>
- Azam, C., Le Viol, I., Julien, J.-F., Bas, Y., & Kerbiriou, C. (2016). Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program. *Landscape Ecology*, 31(10), 2471–2483. <https://doi.org/10.1007/s10980-016-0417-3>
- Boughey, K. L., Lake, I. R., Haysom, K. A., & Dolman, P. M. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. *Biological Conservation*, 144(9), 2300–2310. <https://doi.org/10.1016/j.biocon.2011.06.008>
- Catto, C. M. C., Hutson, A. M., Racey, P. A., & Stephenson, P. J. (1996). Foraging behaviour and habitat use of the serotine bat (*Eptesicus serotinus*) in southern England. *Journal of Zoology*, 238(4), 623–633. <https://doi.org/10.1111/j.1469-7998.1996.tb05419.x>
- Catto, C. M. C., Racey, P. A., & Stephenson, P. J. (1995). Activity patterns of the serotine bat (*Eptesicus serotinus*) at a roost in southern England. *Journal of Zoology*, 235(4), 635–644. <https://doi.org/10.1111/j.1469-7998.1995.tb01774.x>
- Claireau, F., Bas, Y., Pauwels, J., Barré, K., Machon, N., Allegrini, B., Puechmaille, S. J., & Kerbiriou, C. (2019). Major roads have important negative effects on insectivorous bat activity. *Biological Conservation*, 235, 53–62. <https://doi.org/10.1016/j.biocon.2019.04.002>
- Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, E., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., Wang, J., Leetmaa, A., ... Joseph, D. (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, 77(3), 437–472.
- Kemp, M. U., Emiel van Loon, E., Shamoun-Baranes, J., & Bouten, W. (2012). RNCEP: Global weather and climate data at your fingertips: *RNCEP. Methods in Ecology and Evolution*, 3(1), 65–70. <https://doi.org/10.1111/j.2041-210X.2011.00138.x>
- Kolkert, H., Smith, R., Rader, R., & Reid, N. (2020). Insectivorous bats foraging in cotton crop interiors is driven by moon illumination and insect abundance, but diversity benefits from woody vegetation cover. *Agriculture, Ecosystems & Environment*, 302, 107068. <https://doi.org/10.1016/j.agee.2020.107068>

- Kyba, C. C. M., Tong, K. P., Bennie, J., Birriel, I., Birriel, J. J., Cool, A., Danielsen, A., Davies, T. W., Outer, P. N. den, Edwards, W., Ehlert, R., Falchi, F., Fischer, J., Giacomelli, A., Giubbilini, F., Haaïma, M., Hesse, C., Heygster, G., Hölker, F., ... Gaston, K. J. (2015). Worldwide variations in artificial skyglow. *Scientific Reports*, 5, 8409. <https://doi.org/10.1038/srep08409>
- Lacoeuilhe, A., Machon, N., Julien, J.-F., & Kerbiriou, C. (2016). Effects of hedgerows on bats and bush crickets at different spatial scales. *Acta Oecologica*, 71, 61–72. <https://doi.org/10.1016/j.actao.2016.01.009>
- Lang, A. B., Kalko, E. K. V., Römer, H., Bockholdt, C., & Dechmann, D. K. N. (2006). Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia*, 146, 659–666. <https://doi.org/10.1007/s00442-005-0131-3>
- McAney, C. M., & Fairley, J. S. (1988). Activity patterns of the lesser horseshoe bat *Rhinolophus hipposideros* at summer roosts. *Journal of Zoology*, 216(2), 325–338. <https://doi.org/10.1111/j.1469-7998.1988.tb02433.x>
- Robinson, M. F., & Stebbings, R. E. (1997a). Activity of the serotine bat, *Eptesicus serotinus*. *Myotis*, 35, 5–16.
- Robinson, M. F., & Stebbings, R. E. (1997b). Home range and habitat use by the serotine bat, *Eptesicus serotinus*, in England. *Journal of Zoology*, 243(1), 117–136. <https://doi.org/10.1111/j.1469-7998.1997.tb05759.x>
- Vaughan, N., Jones, G., & Harris, S. (1997). Habitat Use by Bats (Chiroptera) Assessed by Means of a Broad-Band Acoustic Method. *The Journal of Applied Ecology*, 34(3), 716–730. <https://doi.org/10.2307/2404918>
- Verboom, B., & Huitema, H. (1997). The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology*, 12, 117–125. <https://doi.org/10.1007/BF02698211>

Supplementary material I: Checks of model assumptions

Model assumptions were tested according to the following procedure: multicollinearity was tested with R package *performance* (VIF below five for each variable and mean VIF below two), spatial and temporal autocorrelations were tested with R package *DHARMa*, QQ-plots were also drawn to assess if distribution choices were sensible. For “timing of activity” analyses, homoscedasticity was assessed with R package *performance*. For “relative abundance” analyses, we plotted standardized residuals against model predictions and controlled zero inflation with R package *DHARM*.

Supplementary material J: Analyses when considering full models without interactions including ALAN

1. Relative abundance

When we did not consider interactions including ALAN, ALAN still was a better predictor of *E. serotinus* relative abundance as its sum of weights (SW) was equal to 0.84 (it was in 73.6% of the models of the model set), compared to artificialized surfaces whose SW was equal to 0.16 (it was in 26.4% of the models of the model set) (Table J.1) (see Table J.2 for details on the model averaging results). Both ALAN and artificialized surfaces estimates were negative, with ALAN one being even lower (-0.0186) than the artificialized surfaces one (-0.0156).

Table J.1: Model averaging results for a delta AICc of six points for the “relative abundance” analyses: estimate, sum of weights (SW) and 95% confidence interval (CI) for each variable (apart from latitude and recorder type that were fixed) (estimates in bold when the 95% confidence interval did not overlap zero and the SW was above 0.60). Results without and with interactions including ALAN are represented so that they might be compared. All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable

Without interactions including ALAN				With interactions including ALAN		
Variables	Estimates	SW	CI (95%)	Estimates	SW	CI (95%)
Temperature	0.0098	1.00	0.0047 ; 0.0150	0.0098	1.00	0.0047 ; 0.0150
Difference_temperature	0.0117	1.00	0.0070 ; 0.0164	0.0118	1.00	0.0071 ; 0.0164
Windspeed	-0.0025	0.47	-0.0061 ; 0.0011	-0.0025	0.47	-0.0060 ; 0.0011
Difference_precipitations	-0.0061	1.00	-0.0097 ; -0.0024	-0.0061	1.00	-0.0098 ; -0.0024
Julian_Day	0.0124	1.00	0.0076 ; 0.0171	0.0124	1.00	0.0077 ; 0.0171
(Julian_Day) ²	-0.0023	0.34	-0.0072 ; 0.0026	-0.0023	0.32	-0.0072 ; 0.0027
Cloud_cover	0.0027	0.63	-0.0008 ; 0.0062	0.0026	0.67	-0.0009 ; 0.0061
Artificialized_surfaces	-0.0156	0.16	-0.0227 ; -0.0086	-0.0156	0.11	-0.0227 ; -0.0086
Grassland	-0.0047	0.50	-0.0114 ; 0.0020	-0.0047	0.50	-0.0114 ; 0.0020
Deciduous_forest	0.0096	1.00	0.0041 ; 0.0151	0.0096	1.00	0.0041 ; 0.0151
Conifer_forest	0.0124	1.00	0.0056 ; 0.0191	0.0124	1.00	0.0057 ; 0.0192

Habitat_diversity	0.0070	0.80	0.0005 ; 0.0134	0.0068	0.82	0.0005 ; 0.0132
Min_distance_freshwater	-0.0039	0.37	-0.0115 ; 0.0037	-0.0039	0.37	-0.0116 ; 0.0037
Small_woody_features	0.0082	1.00	0.0026 ; 0.0138	0.0082	1.00	0.0026 ; 0.0138
ALAN	-0.0186	0.84	-0.0268 ; -0.0104	-0.0186	0.89	-0.0268 ; -0.0104
Moonlight	-0.0064	1.00	-0.0104 ; -0.0024	-0.0065	1.00	-0.0105 ; -0.0025
Difference_temperature :Temperature	0.0009	0.26	-0.0026 ; 0.0045	0.0009	0.24	-0.0026 ; 0.0045
Cloud_cover:Moonlight	0.0015	0.21	-0.0017 ; 0.0048	0.0015	0.21	-0.0017 ; 0.0047
ALAN:Cloud_cover				-0.0011	0.14	-0.0056 ; 0.0035
Moonlight:ALAN				-0.0006	0.19	-0.0048 ; 0.0036

Table J.2: Results of the model averaging for the “relative abundance” and the “timing of activity” analyses without interactions including ALAN. Even if a lot of models were selected in these analyses, the differences between the AICc of the null model and the AICc of the best model were always high.

	Number of models in a Δ AICc of 6	AICc of the best model	AICc of the null model	AICc null model* – AICc best model
Relative abundance	216	10,542	10,796	254
Timing of activity	130	27,840	27,991	151

*include random effects for “relative abundance” and “timing of activity” analyses, include the weight on the logarithm of the number of *E. serotinus* passes for “timing of activity” analyses.

2. Timing of activity

When we did not consider interactions including ALAN, ALAN still was a better predictor of the median time of activity as its SW was equal to 0.997 (it was in 99.2% of the models of the model set), compared to artificialized surfaces whose SW was equal to 0.003 (it was in 0.8% of the models of the model set) (Table J.3) (see Table J.2 for details on the model averaging results). Furthermore, both ALAN and artificialized surfaces estimates were positive, with ALAN one being even greater (0.218) than the artificialized surfaces one (0.171).

Table J.3: Model averaging results for a delta AICc of six points for the “timing of activity” analyses: estimate, sum of weights (SW) and 95% confidence interval (CI) for each variable (apart from latitude and the autocovariate that were fixed) (estimates in bold when the 95% confidence interval did not overlap zero and the SW was above 0.60). Results without and with interactions including ALAN are both represented so that they might be compared. All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable

	Without interactions including ALAN			With interactions including ALAN		
Variables	Estimates	SW	CI (95%)	Estimates	SW	CI (95%)
Temperature	0.042	0.36	-0.037 ; 0.12	0.031	0.31	-0.047 ; 0.110
Difference_temperature	0.112	1.00	0.059 ; 0.165	0.114	1.00	0.064 ; 0.165
Windspeed	-0.089	1.00	-0.133 ; -0.046	-0.093	1.00	-0.136 ; -0.050
Difference_precipitations	-0.052	0.90	-0.098 ; -0.005	-0.053	0.91	-0.099 ; -0.006
Julian_Day	-0.017	1.00	-0.104 ; 0.071	-0.031	1.00	-0.119 ; 0.057
(Julian_Day) ²	0.154	1.00	0.077 ; 0.231	0.142	1.00	0.061 ; 0.223
Cloud_cover	-0.155	1.00	-0.199 ; -0.111	-0.155	1.00	-0.199 ; -0.110
Artificialized_surfaces	0.171	0.00	0.061 ; 0.28	NA	NA	NA
Grassland	0.004	0.17	-0.115 ; 0.123	0.012	0.18	-0.111 ; 0.135
Deciduous_forest	-0.057	0.26	-0.186 ; 0.072	-0.059	0.26	-0.189 ; 0.072
Conifer_forest	-0.025	0.20	-0.145 ; 0.095	-0.017	0.18	-0.138 ; 0.104
Habitat_diversity	0.023	0.19	-0.082 ; 0.128	0.017	0.18	-0.090 ; 0.123
Min_distance_freshwater	0.031	0.20	-0.116 ; 0.177	0.041	0.20	-0.107 ; 0.190
Small_woody_features	-0.057	0.32	-0.169 ; 0.056	-0.067	0.36	-0.181 ; 0.047
ALAN	0.218	1.00	0.102 ; 0.335	0.235	1.00	0.117 ; 0.354
Moonlight	0.076	0.99	0.016 ; 0.136	0.092	1.00	0.032 ; 0.152
Difference_temperature :Temperature	-0.008	0.05	-0.05 ; 0.034	-0.024	0.09	-0.066 ; 0.019
Cloud_cover:Moonlight	-0.008	0.18	-0.05 ; 0.035	-0.013	0.21	-0.055 ; 0.030
ALAN:Cloud_cover				0.059	0.95	0.011 ; 0.106
Moonlight:ALAN				-0.073	1.00	-0.120 ; -0.027

Supplementary material K: Checking of the robustness of the model averaging results

1. Comparison between the model averaging approach and the model selection one

Relative abundance

The best model obtained with the dredge (i.e., the one with the lowest AICc – second order bias correction for Akaike Information Criterion) was the following one:

$$\begin{aligned} \text{Relative abundance metric} \sim & \text{Conifer_forest} + \text{Deciduous_forest} + \text{Julian_day} + \text{Moonlight} + \\ & \text{Small_woody_features} + \text{Habitat_diversity} + \text{ALAN} + \text{Cloud_cover} + \text{Eq. (K.1)} \\ & \text{Difference_precipitations} + \text{Difference_temperature} + \text{Temperature} + \text{Latitude} + \\ & \text{Recorder_type} + (1 \mid \text{site} / \text{participation}) \end{aligned}$$

As shown in Table K.1, the estimates (standardized) of the best model were highly similar to those obtained with the model averaging. The variables that had a sum of weights (SW) above 0.60 and whose 95% interval did not overlap zero were all in the best model and their p-value was significant. Hence, the model averaging and the model selection approaches were consistent. Our conclusions would have been the same whatever the approach chosen.

Table K.1: Comparison between the result obtained with a model selection approach (model with the lowest AICc) and the model averaging approach for the “relative abundance” analyses. In bold, in the column “estimates best model”, are the estimates whose p-value was below 0.05 (Anova II). In bold, in the column “estimates model averaging”, are the estimate whose SW were above 0.6 and whose 95% confidence interval did not overlap 0. (In this table we did not put latitude and recorder type that were fixed for “relative abundance” analyses). All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable

Variables	Estimates best model	p-value	Estimates model averaging	SW > 0.60 and 95% interval did not overlap 0
Temperature	0.0101	8.7e-05***	0.0098	Yes
Difference_temperature	0.0117	5.4e-07***	0.0118	Yes
Windspeed	NA	NA	-0.0025	No
Difference_precipitations	-0.0063	6.9e-04***	-0.0061	Yes
Julian_Day	0.0127	2.8e-08***	0.0124	Yes
(Julian_Day) ²	NA	NA	-0.0023	No
Cloud_cover	0.0027	1.2e-01	0.0026	No
Artificialized_surfaces	NA	NA	-0.0156	No
Grassland	NA	NA	-0.0047	No
Deciduous_forest	0.0101	1.0e-04***	0.0096	Yes
Conifer_forest	0.0134	9.8e-06***	0.0124	Yes
Habitat_diversity	0.0074	1.1e-02*	0.0068	Yes
Min_distance_freshwater	NA	NA	-0.0039	No
Small_woody_features	0.0074	5.0e-03**	0.0082	Yes
ALAN	-0.0167	1.5e-06***	-0.0186	Yes
Moonlight	-0.0063	1.9e-03**	-0.0065	Yes
Difference_temperature :Temperature	NA	NA	0.0009	No
Cloud_cover:Moonlight	NA	NA	0.0015	No
ALAN:Cloud_cover	NA	NA	-0.0011	No
Moonlight:ALAN	NA	NA	-0.0006	No

Timing of activity

The best model obtained with the dredge (i.e., the one with the lowest AICc) was the following one:

$$\begin{aligned} \text{Timing of activity metric} \sim & \text{Julian_day} + \text{Julian_day}^2 + \text{Moonlight} + \text{ALAN} + \text{Cloud_cover} + \\ & \text{Difference_precipitations} + \text{Difference_temperature} + \text{Wind_speed} + \\ & \text{Latitude} + \text{autocov} + \text{Moonlight} : \text{ALAN} + \text{ALAN} : \text{Cloud_cover} + (1 \mid \text{site}) \end{aligned} \quad \text{Eq. (K.2)}$$

As shown in Table K.2, the estimates (standardized) of the best model were highly similar to those obtained with the model averaging. The covariates that had a sum of weights (SW) above 0.60 and whose 95% interval did not overlap zero were all in the best model and their p-value was significant. Hence, the model averaging and the model selection approaches were consistent. Our conclusions would have been the same whatever the approach chosen.

Table K.2: Comparison between the result obtained with a model selection approach (model with the best AICc) and the model averaging approach for the “timing of activity” analyses. In bold, in the column “estimates best model”, are the estimate whose p-value was below 0.05 (Anova II). In bold, in the column “estimates model averaging”, are the estimates whose SW were above 0.6 and whose 95% confidence interval did not overlap 0. (In this table we did not put latitude and the autocovariate that were fixed for “timing of activity” analyses). All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable

Variables	Estimates best model	p-value	Estimates model averaging	SW > 0.60 and 95% interval did not overlap 0
Temperature	NA	NA	0.031	No
Difference_temperature	0.120	5.6e-08***	0.114	Yes
Windspeed	-0.093	2.3e-05***	-0.093	Yes
Difference_precipitations	-0.052	2.4e-02*	-0.053	Yes
Julian_Day	-0.027	5.3e-01	-0.031	No
(Julian_Day) ²	0.140	5.7e-04***	0.142	Yes
Cloud_cover	-0.153	1.4e-12***	-0.155	Yes
Artificialized_surfaces	NA	NA	NA	NA

Appendices – Appendix II

Grassland	NA	NA	0.012	No
Deciduous_forest	NA	NA	-0.059	No
Conifer_forest	NA	NA	-0.017	No
Habitat_diversity	NA	NA	0.017	No
Min_distance_freshwater	NA	NA	0.041	No
Small_woody_features	NA	NA	-0.067	No
ALAN	0.233	1.5e-04***	0.235	Yes
Moonlight	0.092	8.7e-03**	0.092	Yes
Difference_temperature :Temperature	NA	NA	-0.024	No
Cloud_cover:Moonlight	NA	NA	-0.013	No
ALAN:Cloud_cover	0.058	1.7e-02*	0.059	Yes
Moonlight:ALAN	-0.074	1.6e-03**	-0.073	Yes

2. Complex model issue

For the model averaging, we chose not to follow Richards et al., (2011) parsimonious approach consisting in post hoc elimination of models that are more complex versions of any model with a lower AICc value. As a matter of fact, it would have been very time-consuming (our model sets were composed of 373 models for the “relative abundance” analyses and 142 models for the “timing of activity” analyses) and, according to Symonds & Moussalli, (2011), it was uncertain if such a method would have consistently improved the model averaging ; whereas Grueber et al. (2011) underlined that some complex models may be composed of unique predictor variables of potentially strong ecological importance that should not be removed in such cases.

Nonetheless, because we did not discard these complex models, there was a risk of overweighting the predictor variables contained in overly complex models. However, as we presented in the first part of this Supplementary materiel (*Comparison between the model averaging approach and the model selection one*), for both analyses the best models already contained all the variables for which we found an effect with the model averaging approach. Hence, none of these variables would have been discarded by following Richards et al. (2011) approach.

However, Richards et al. (2011) parsimonious approach could potentially change the sum of weights (SW) and confidence interval of these variables. Nonetheless, for the “relative abundance” analyses, almost all variables which had an effect according to our model averaging approach ($SW > 0.60$ and a 95% confidence interval that did not overlap 0), were in all the models of the models set (373 models) and their p-value was significant in all these models. The exceptions were (1) small woody features but it was in 99.5% of the models and its p-value was significant in all these models; (2) habitat diversity which was a variable that was not discussed in the main text, it had just been added to control potential effect of landscape structure on bat abundance; (3) and ALAN but the models in which this variable was not were those with artificialized surfaces, with no model containing neither of these two variables, ALAN was significant in all the models in which it was included (Table K.3).

Likewise, for the “timing of activity” analyses, almost all variables that had effect with our model averaging approach were also included in all the models selected in the model set used for the model averaging and their p-value was significant in all these models. The exceptions were difference of precipitations and the interaction between cloud cover and ALAN, but there were nonetheless in a high percentage of models (respectively 87.3% and 92.3%) and their p-values were significant in all the models in which they were included (Table K.4).

Moreover, as shown in Figure K.2 and K.3 of the third part of this Supplementary material (*Multicollinearity effect on coefficient estimates*), the estimates of the variables which had an effect according to our model averaging approach were quite similar in all the models selected in the model set of the model averaging for both analyses. For both analyses, in all the models including ALAN, the absolute value of its estimate was greater than those of the other variables. Hence, we are confident that Richards et al. (2011) approach would have resulted in the same variable selection, in similar estimates, and that ALAN would have stayed the variable whose estimate was the greater in absolute value.

Table K.3: Comparison between the obtained results when considering all the models within a $\Delta AICc$ of six points individually and the results of the model averaging for the “relative abundance” analyses. In bold are the estimates whose SW were above 0.6 and whose 95% confidence interval did not overlap 0. (In this table we did not put latitude and recorder type that were fixed for “relative abundance” analyses). All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable

Variables	Estimates model averaging	SW > 0.60 and 95% interval did not overlap 0	Percentage of models in the model averaging	Percentage of models in which the p-value is <0.05
Temperature	0.0098	Yes	100	100
Difference_temperature	0.0118	Yes	100	100
Windspeed	-0.0025	No	48.0	0
Difference_precipitations	-0.0061	Yes	100	100
Julian_Day	0.0124	Yes	100	100
(Julian_Day) ²	-0.0023	No	40.5	0
Cloud_cover	0.0026	No	71.0	0
Artificialized_surfaces	-0.0156	No	15.3	15.3
Grassland	-0.0047	No	55.5	11.8
Deciduous_forest	0.0096	Yes	100	100
Conifer_forest	0.0124	Yes	100	100
Habitat_diversity	0.0068	Yes	74.5	55.5
Min_distance_freshwater	-0.0039	No	44.2	0
Small_woody_features	0.0082	Yes	99.5	99.5
ALAN	-0.0186	Yes	84.7	84.7
Moonlight	-0.0065	Yes	100	100
Difference_temperature :Temperature	0.0009	No	32.3	0
Cloud_cover:Moonlight	0.0015	No	27.1	0
ALAN:Cloud_cover	-0.0011	No	19.3	0
Moonlight:ALAN	-0.0006	No	26.8	0

Table K.4: Comparison of the obtained results when considering all models within a ΔAIC_c of six points individually with the results of the model averaging for the “timing of activity” analyses. In bold are the estimate coefficient whose SW were above 0.6 and whose 95% confidence interval did not overlap 0. (In this table we did not put latitude and the autocovariate that were fixed for “timing of activity” analyses). All quantitative fixed effects were scaled and estimates were standardized by dividing them by the standard deviation of the response variable

Variables	Estimates model averaging	SW > 0.60 and 95% interval did not overlap 0	Percentage of models in the model averaging	Percentage of models in which the p-value is <0.05
Temperature	0.031	No	32.3	0
Difference_temperature	0.114	Yes	100	100
Windspeed	-0.093	Yes	100	100
Difference_precipitations	-0.053	Yes	87.3	87.3
Julian_Day	-0.031	No	100	0
(Julian_Day) ²	0.142	Yes	100	100
Cloud_cover	-0.155	Yes	100	100
Artificialized_surfaces	NA	NA	NA	NA
Grassland	0.012	No	24.6	0
Deciduous_forest	-0.059	No	32.4	0
Conifer_forest	-0.017	No	23.9	0
Habitat_diversity	0.017	No	23.2	0
Min_distance_freshwater	0.041	No	25.4	0
Small_woody_features	-0.067	No	38.7	0
ALAN	0.235	Yes	100	100
Moonlight	0.092	Yes	100	100
Difference_temperature :Temperature	-0.024	No	11.3	0
Cloud_cover:Moonlight	-0.013	No	26.1	0
ALAN:Cloud_cover	0.059	Yes	92.3	92.3
Moonlight:ALAN	-0.073	Yes	100	100

3. *Multicollinearity effect on coefficient estimates*

According to Cade (2015), the presence of multicollinearity leads to different scaling of units for the regression coefficient of a given predictor variable across candidate models with different combinations of predictor variables. To solve this issue and ensure that multimodel inferences are sound, he suggested to standardize estimates based on partial standard deviations.

By excluding predictor variables that were responsible for multicollinearity (difference of windspeed, sum of precipitations of the day, crops, road density) and by never including artificialized surfaces and ALAN in the same models, we ensured that the variance inflation factor (VIF) of our predictor variables and the mean VIF of our models would stay very low. However, Cade (2015) suggested that even when the VIFs are low, there might be changes in the scaling of predictors under different model covariance structures.

Hence, as suggested by Cade (2015), we decided to standardised estimates based on partial standard deviations for their variables. As this method was not implemented in the *model.avg* and the *dredge* functions (R package *MuMIn*) for models fitted with the function *glmmTBM* (R package *glmmTMB*), we did it by following the procedure shown in Figure K.1. As shown in Table K.5, Figure K.2 and Figure K.3, such standardisation did not change our conclusions: ALAN still was the covariate whose estimate was the highest in absolute value for both analyses. For the “relative abundance” analyses, ALAN estimate was higher than the estimate of artificialized surfaces. Furthermore, even if the standardisation based on partial standard deviation reduced the absolute values of the estimates, their values remained close to those obtained with a “classical” standardisation such as the one used in the main text.

For each covariate (*i*)

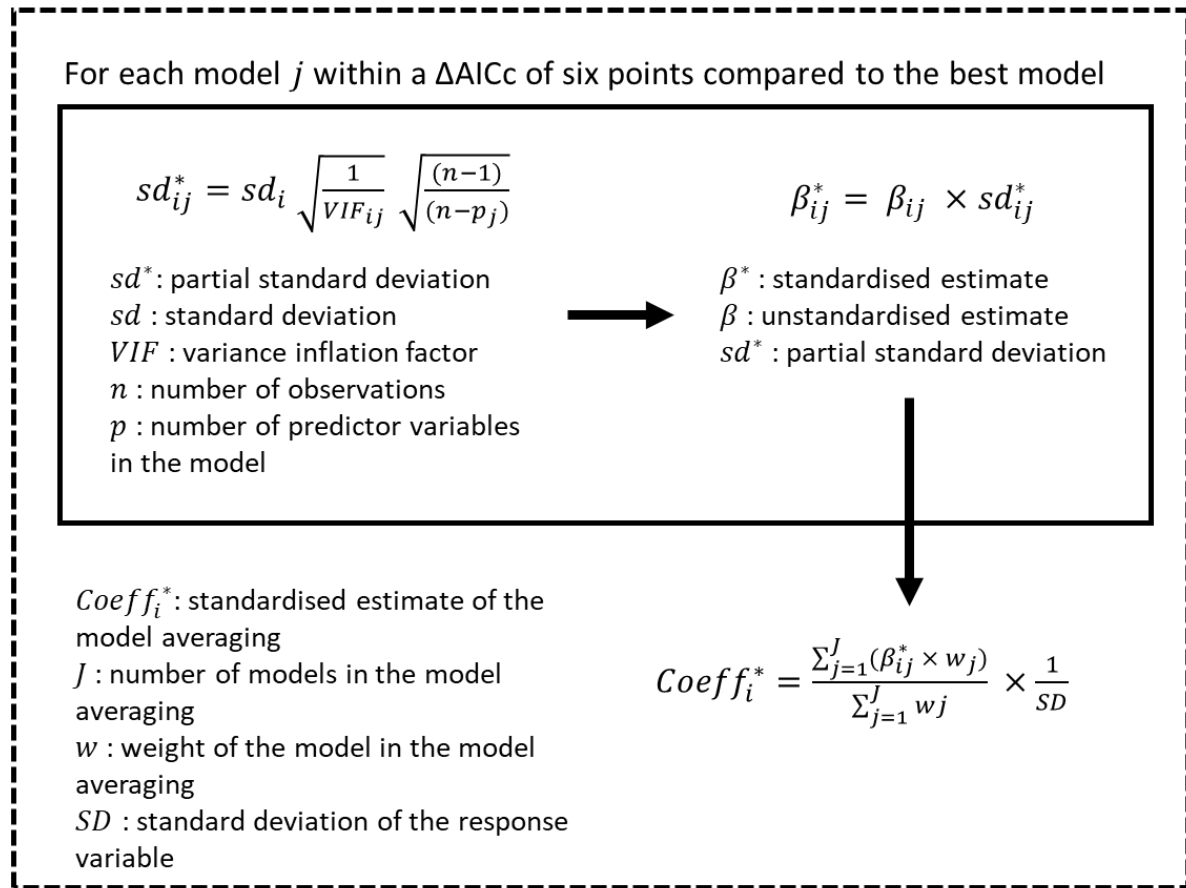


Figure K.1: Procedure followed to standardised estimates based on partial standard deviations in the model averaging (Cade, 2015)

Table K.5: Comparison of the obtained coefficient estimates with the model averaging with a “classical” standardisation of the coefficient estimates and with a standardisation based on partial standard deviations for the “relative abundance” and “timing of activity” analyses (estimates are in bold when the 95% confidence interval did not overlap zero and the SW was above 0.60). (In this table we did not put latitude and recorder type that were fixed for “relative abundance” analyses and latitude and the autocovariate that were fixed for “timing of activity” analyses)

Variables	Relative abundance		Timing of activity	
	Classical	SD partial	Classical	SD partial
Temperature	0.0098	0.0072	0.031	0.022
Difference_temperature	0.0118	0.0088	0.114	0.103
Windspeed	-0.0025	-0.0024	-0.093	-0.089
Difference_precipitations	-0.0061	-0.0058	-0.053	-0.051
Julian_Day	0.0124	0.0114	-0.031	-0.024
(Julian_Day) ²	-0.0023	-0.0020	0.142	0.110
Cloud_cover	0.0026	0.0025	-0.155	-0.144
Artificialized_surfaces	-0.0156	-0.0122	NA	NA
Grassland	-0.0047	-0.0037	0.012	0.010
Deciduous_forest	0.0096	0.0082	-0.059	-0.051
Conifer_forest	0.0124	0.0086	-0.017	-0.013
Habitat_diversity	0.0068	0.0053	0.017	0.016
Min_distance_freshwater	-0.0039	-0.0033	0.041	0.041
Small_woody_features	0.0082	0.0069	-0.067	-0.062
ALAN	-0.0186	-0.0146	0.235	0.223
Moonlight	-0.0065	-0.0064	0.092	0.086
Difference_temperature :Temperature	0.0009	0.0009	-0.024	-0.022
Cloud_cover:Moonlight	0.0015	0.0015	-0.013	-0.013
ALAN:Cloud_cover	-0.0011	-0.0010	0.059	0.057
Moonlight:ALAN	-0.0006	-0.0006	-0.073	-0.070

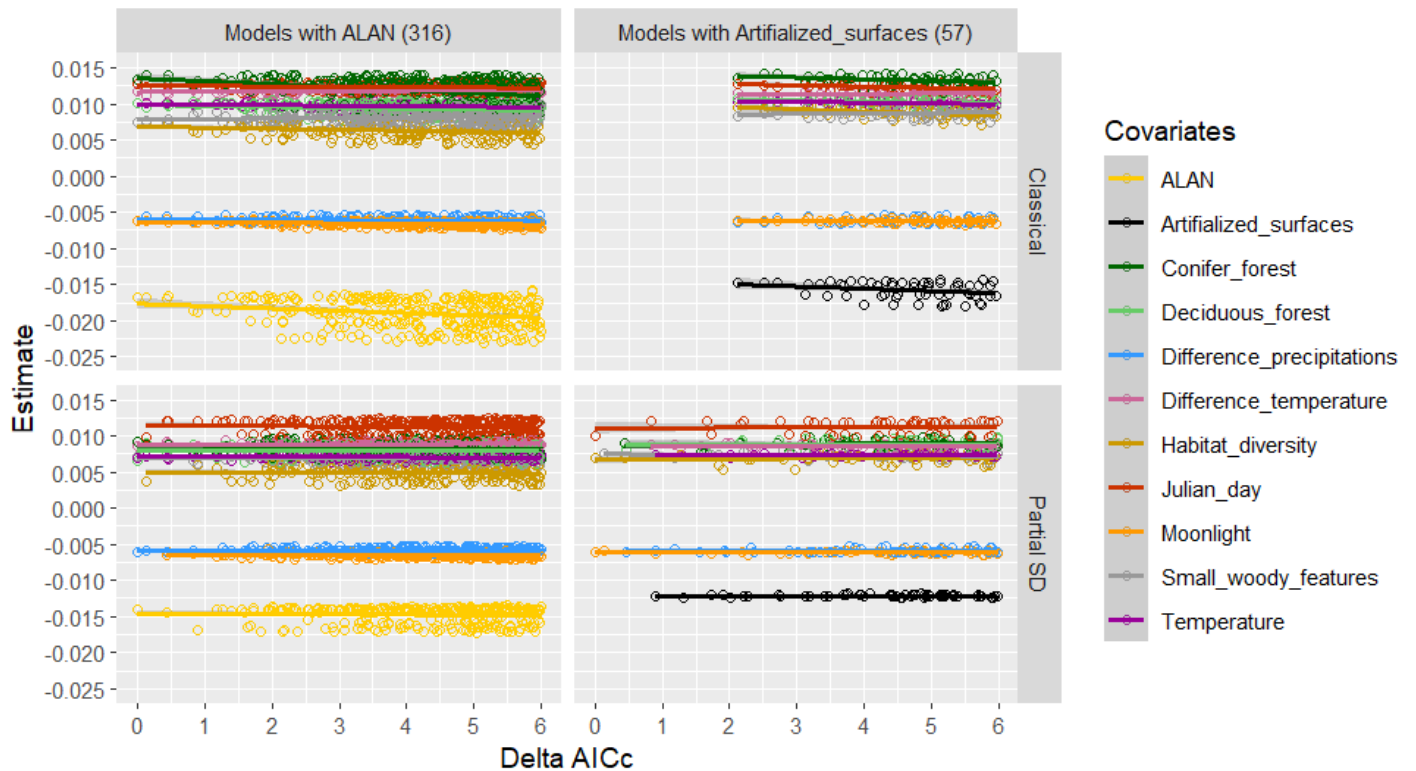


Fig K.2: For the “relative abundance” analyses, variations of the values of the estimates in the 373 models within a $\Delta AICc$ of six points compared to the best model. Only the variables which had an effect according to the model averaging approach are represented. Their estimates are represented according to the $\Delta AICc$ of the model in which they have been estimated. The solid curves represent the result of generalized linear models fitted to the data. The left panels correspond to all the models in which ALAN was selected and the right panels correspond to all the models in which artificialized surfaces were selected. There was no model with neither ALAN nor artificialized surfaces. The upper panels correspond to “classical” standardised estimates and the lower panels correspond to standardised estimates based on partial standard deviations.

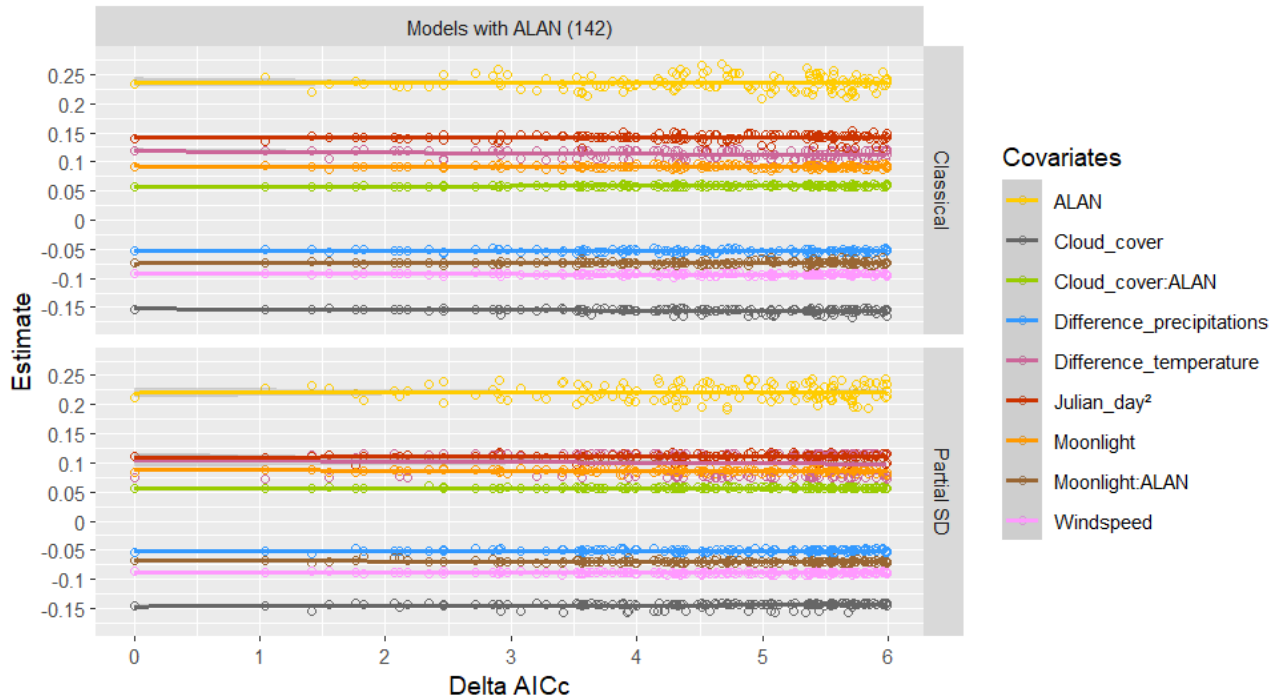


Fig K.3: For the “timing of activity” analyses, variations of the values of the estimates in the 142 models within a $\Delta AICc$ of six points compared to the best model. Only the covariates which had an effect according to the model averaging approach are represented. Their estimates are represented according to the $\Delta AICc$ of the model in which they have been estimated. The solid curves represent the result of generalized linear models fitted to the data. ALAN was selected over artificialized surfaces in all models. The upper panels correspond to “classical” standardised estimates and the lower panels correspond to standardised estimates based on partial standard deviations.

Bibliography

- Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, 96(9), 2370–2382. <https://doi.org/10.1890/14-1639.1>
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions: Multimodel inference. *Journal of Evolutionary Biology*, 24(4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>
- Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65(1), 77–89. <https://doi.org/10.1007/s00265-010-1035-8>
- Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology*, 65(1), 13–21. <https://doi.org/10.1007/s00265-010-1037-6>

Table L: Results of the model averaging for the “relative abundance” and the “timing of activity” analyses. Even if a lot of models were selected in these analyses, the differences between the AICc of the null model and the AICc of the best model were always high.

	Number of models in a Δ AICc of 6	AICc of the best model	AICc of the null model	AICc null model* – AICc best model
Relative abundance	373	10,542	10,796	254
Timing of activity	142	27,831	27,991	160

*include random effects for “relative abundance” and “timing of activity” analyses, include the weight on the logarithm of the number of *E. serotinus* passes for “timing of activity” analyses.

Table M: Mean of the mean radiances (in $\text{nW}\cdot\text{sr}^{-1}\cdot\text{cm}^{-2}$) of the French municipalities according to their population size (only municipalities that are below 500 m above sea levels are considered).

Population	Mean of the mean radiances	Number of municipalities
> 900,000	62.83	1 (Paris)
]200,000 ; 900,000]	39.7	10
]50,000 ; 200,000]	35.5	103
]10,000 ; 50,000]	19.6	802
]5000 ; 10,000]	7.8	1122
]1000 ; 5000]	2.2	7446
]500 ; 1000]	0.75	6537
]100 ; 500]	0.35	14,959
< 100	0.24	3458

Figure N: Interaction between cloud cover and ALAN: Predicted values and 95% confidence intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they were previously scaled) apart from cloud cover and ALAN.

This graph represents the median time of activity according to cloud cover (back transformed in %) for three values of ALAN (2.2 nW.sr⁻¹.cm⁻² being the mean radiance of French municipalities of 1000 to 5000 inhabitants and 7.8 nW.sr⁻¹.cm⁻² being the mean radiance for municipalities of 5000 to 10,000 inhabitants, see Table M).

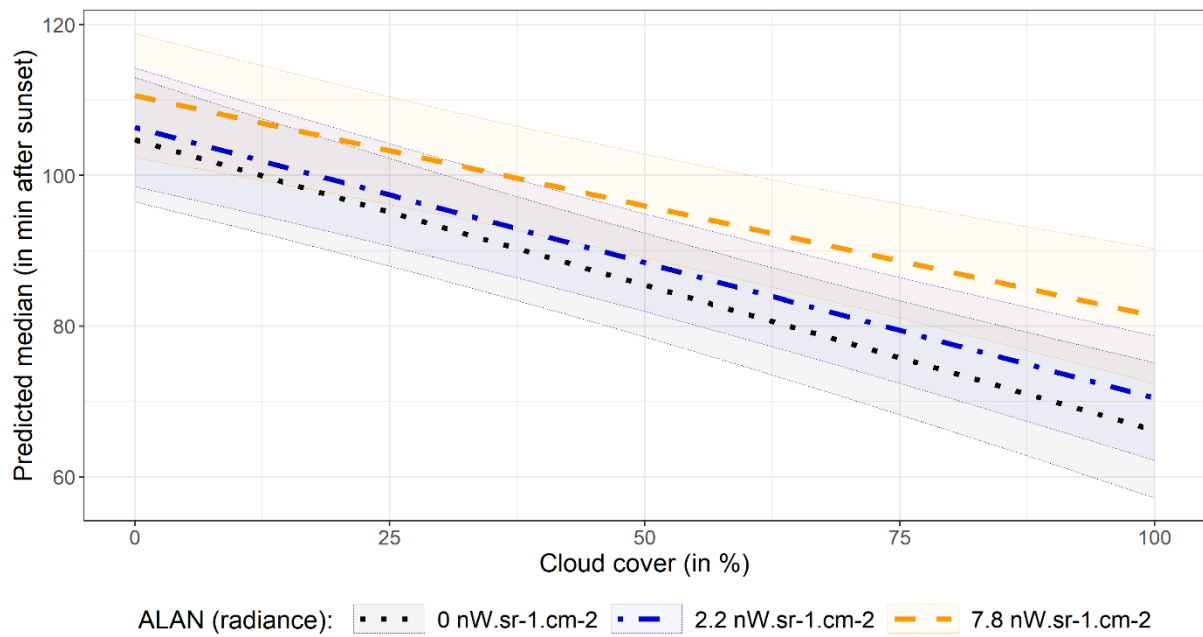
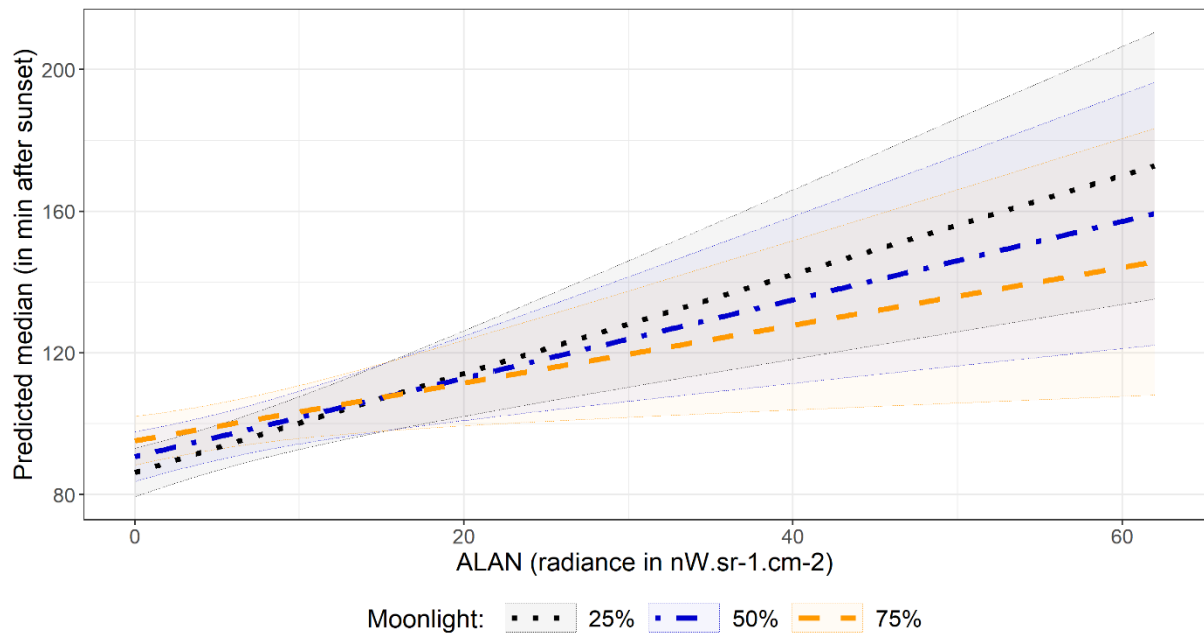


Figure O: Interaction between ALAN and moonlight: Predicted values and 95% confidence intervals of the timing of activity (i.e., the time of the median *E. serotinus* pass during the first half of the night) with all variables equal to zero (i.e., all variables equal to their mean, as they were previously scaled) apart from ALAN and moonlight. This graph represents the median time of activity according to ALAN (radiance back transformed in $\text{nW} \cdot \text{sr}^{-1} \cdot \text{cm}^{-2}$) for three values of moonlight.



Appendix III: Supplementary information on *Impact of light pollution on the abundance and timing of activity of open- and edge-space-foraging bat species at landscape scale (in prep)*

- **Biological data:** Vigie-Chiro dataset

- **Data curation:** (1) Sites within the known distribution range, (2) All sites separated by at least 50 m, (3) Only passes with a confidence index value > 0.5 , (4) *For the analysis on the timing:* nights with a least a given number of passes of the species, this number being determined based on the method presented in the Supplementary material B of Mariton et al. (2022) (in the Appendix II of this manuscript).
- **Periods:** Gestation (April 15 – June 21) & Lactation (June 22 – August 21)
- **Biological metrics:** number of bat passes (hereafter called relative abundance) & time of the median pass during the first part of the night (hereafter noted TMedianP1).

- **Statistical analyses:** similar to those of Mariton et al. (2022)

Relative abundance / TMedianP1 ~ Latitude + Latitude² + meteorological metrics (of the day and the previous days) + landscape metrics (landuse, heterogeneity, water, hedges) + cloud cover + moon illumination + ALAN + recorder type (only for abundance)

- **For the relative abundance:** (1) Random effect on participations nested on sites, (2) Distribution: negative binomial.
- **For the timing of activity:** (1) Random effect on sites, (2) Distribution: gaussian, (3) Weight: $\log(1 + \text{number of passes during the first part of the night})$
- **Dredge** (never including the percentage of artificialized surfaces and ALAN in the same models) and **model averaging** within a ΔAIC of 6

Appendix IV: Online appendices of Kerbiriou et al. (2020)

Supplementary Material 1: Radiometric and Photometric Quantities

It is of major importance to distinguish radiometric quantities (energetic) which describe the energy transport and its spatial distribution from Electromagnetic Radiation (EM) and photometric quantities (visual) which express energy transport and it's the spatial distribution of light only as perceived by the human eye (visible part of EM spectrum ranging from 360nm to 780 nm).

An electric light source that receives an Input Electrical Power, P_{in} (measured in W), will transform a part of that power in radiation emission distributed among all wavelengths, λ , EM spectrum, this is called Radiant Spectral Distribution, $\Phi(\lambda)$ (measured in $W \cdot nm^{-1}$). The integral of this quantity among all EM spectrum wavelengths is called the Radiant Flux (or Radiant Power), Φ_e (measured in W); $\Phi_e = \int \Phi(\lambda) d\lambda$. The ratio between the Radiant Flux over the Input Electrical Power in the lamp, is known as the Radiant Efficiency of the light source, ϵ , and is expressed in percentage (%).

When the Radiant Spectral Distribution is perceived by the human eye it is “selectively filtered” following the spectral response *of the eye*. This spectral response, depends also on the surrounding quantity of light. We can speak in terms of Photopic Luminosity Function, $V(\lambda)$, when enough light is available (daylight or standard indoor lighting conditions), on the opposite, when very few light is available (eg. starlight only) we speak about Scotopic Luminosity Function, $V'(\lambda)$. All intermediate situations (eg. twilight) are known as mesopic conditions and described by a series of $V_m(\lambda)$ functions depending, among others, on the surrounding quantity of light. All the Luminosity Functions above are standardized by the International Commission on Illumination (CIE); all of them are strictly equal to zero beyond the visible radiation limits. The Luminosity Function is used to switch from Radiometric to Photometric quantities. Thus, we define:

The Luminous Flux, Φ_v , measured in lumens (lm) is defined as a proportion of the integral of the product of the Radiant Spectral Distribution by the luminosity function: $\Phi_v = K_{cd} \int \Phi(\lambda) V(\lambda) d\lambda$, where the proportionality constant, K_{cd} , is one of the 7 fundamental constants of SI-unit system (redefined in 2019) and it is equal to $683 \text{ lm} \cdot W^{-1}$ (it can be seen, as the luminous flux induced by 1 W of monochromatic radiant power at 555 nm). The ratio

between the Luminous Flux over the Input Electrical Power in the lamp, is known as the Luminous Efficacy of the light source, η , and is expressed in lumens per watt (lm.W^{-1}).

When a part of the flux (radiant or luminous), $d\Phi_{(e \text{ or } v)}$, is directed towards a specific direction within a beam defined by a solid angle $d\Omega$ (expressed in steradians, sr), the ratio $d\Phi_{(e \text{ or } v)}/d\Omega$ is called either Radiant Intensity, I_e (expressed in W.sr^{-1}) in radiometry, or luminous Intensity, I_v (expressed in lm.sr^{-1} , or, in candelas -cd- which is the official unit) in photometry.

When a part of the flux (radiant or luminous), $d\Phi_{(e \text{ or } v)}$, irradiates/illuminates a surface element dS , the ratio $d\Phi_{(e \text{ or } v)}/dS$ is called either Irradiance, E_e (expressed in W.m^{-2}) in radiometry, or Illuminance, E_v (expressed in lm.m^{-2} , or, in lux -lx- which is the official unit) in photometry.

When a part of the flux (radiant or luminous), $d\Phi_{(e \text{ or } v)}$, originating from a single direction defined by a solid angle $d\Omega$, hits a surface element dS the quantity $dI_{(e \text{ or } v)}/dS$ is called either Radiance, L_e (expressed in $\text{W.sr}^{-1}.\text{m}^{-2}$) in radiometry, or, Luminance, L_v (expressed in $\text{lm.sr}^{-1}.\text{m}^{-2}$, or, in cd.m^{-2} which is the official unit) in photometry. In some case, in photometry, the term Brightness or Luminosity are also used to define that quantity, but the second is obsolete and must be avoided. Luminance is a very important quantity for photometry because it is the attribute of a visual sensation according to which an area appears to emit more or less light.

All the defined quantities above, radiometric or photometric, are integrated among wavelength, but, in some cases, we may need to use them for specific wavelengths, in that cases the qualificative “spectral” has to be added to the quantity name to differentiate it from integral quantities. For our study, the integral quantities are more relevant.

Photometric quantities are relevant to define indoor/outdoor artificial lighting systems performance and design the system. However, there are fully meaning less for animals for whose visual response could be different from that of human beings.

In most cases basic photometric instruments (lux-meters and luminance-meters) are designed and calibrated to measure photometric quantities (respectively, illuminance and luminance) under Photopic conditions. Hence, when light level is not sufficient (mesopic or even scotopic conditions) the values obtained are not representative of the reality even for the human eye. This can be the case in outdoor lighting especially in remote areas. Further, all lighting standards for indoor and outdoor lighting assume photopic conditions only.

Appendices – Appendix IV

All the above description is based on IEC (International Electrotechnical Commission) vocabulary (IEC 60050) as can be found in:

<http://www.electropedia.org/iev/iev.nsf/index?openform&part=845>

Supplementary Material 2: Composition of landscape variables and streetlight column characteristics among sites.

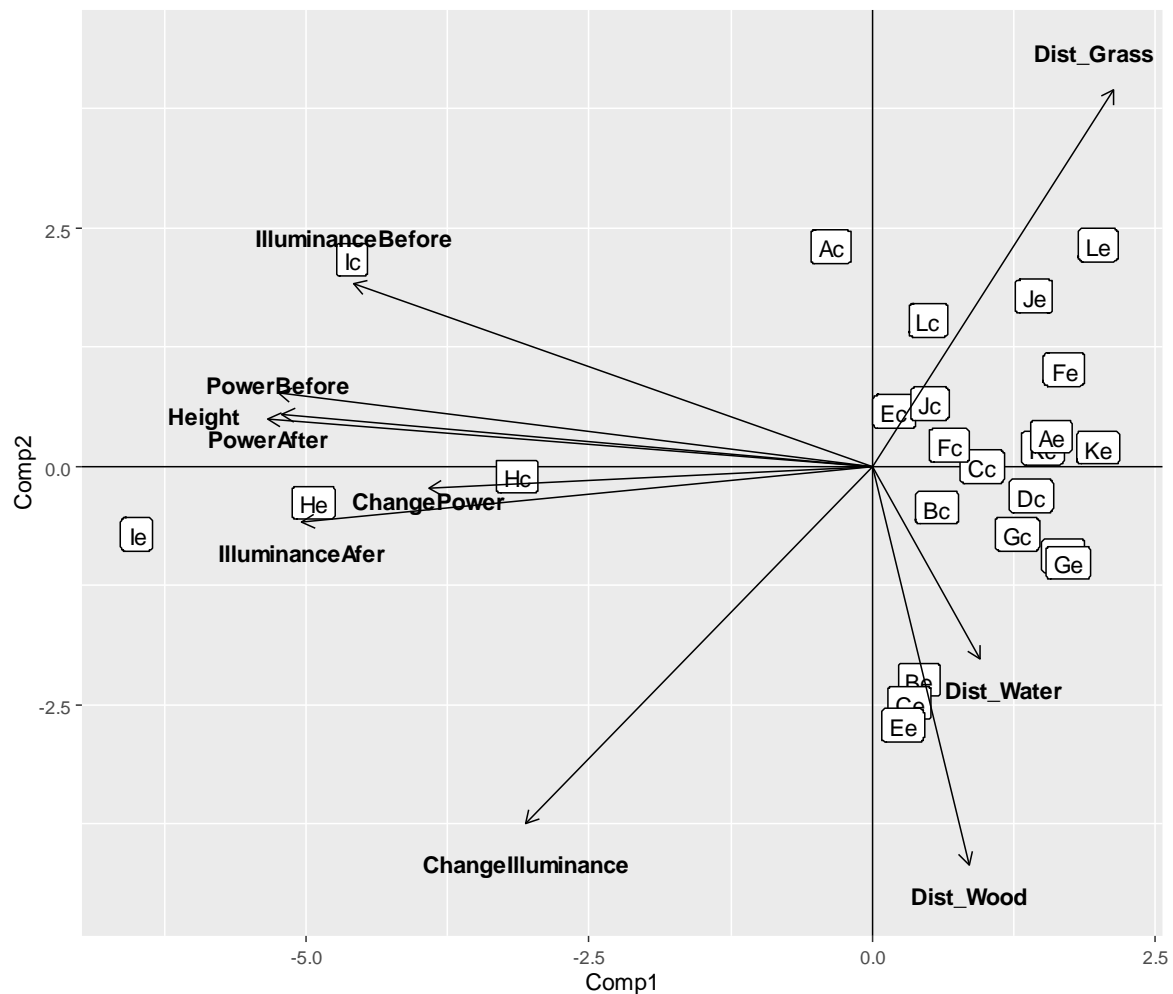


Figure S1. Principal Component Analysis (R Package ade4, function dudi.pca, Chessel D. & Dufour AB) performed on landscape variables and streetlight column characteristics among sites (Ac: control lighting column of the pair A, Ae: experimental lighting column of the pair A). The streetlight characteristics included characteristics that did not change such as the lighting height (Height) and characteristics that changed during the switch such as power and illuminance: PowerBefore is the power (Watts) in site before the switch, PowerAfter, power after the switch (same typology for illuminance), ChangePower is the difference between the power of LPS in experimental site before the switch and the power of LED after the switch (same definition for the ChangeIlluminance). Landscape variables included the distance to a wooded area (m), Dist_Wood, the distance to freshwater (m) Dist_Water, and the distance to grassland (m), Dist_Grass. (a) eigenvalues of the PCA.

Supplementary Material 3: Comparison of the results of parametric and non-parametric approaches when changes in light intensity are not taken into account

Statistical analysis

We ran Generalized Linear Mixed-effects Models (GLMMs R package glmmTMB) focused on the changes in bat activity between before and after switch-over periods for control and experimental lighting columns, without considering changes in light intensity (power or illuminance). According to the response variable: the number of bat passes or buzz ratio, we used respectively a negative binomial and binomial distribution. As fixed explanatory variables we included in our model the type of lighting column (*i.e.* control or experimental), the period (*i.e.* before or after the switch-over) and the interaction between the type of site and period. We used a nested random effect (site) to account for the structure of the BACIP data (*i.e.* a control and experimental pair sampled inside a site). The statistical models were thus structured as follows:

$$\text{Bat activity} \sim \text{Type of column} * \text{Period} + (1|\text{site})$$

Where *Bat activity* was the total number of bat passes, or the number of bat passes for a given species or the feeding buzz ratio, *Type of column* was either the control or the experimental lighting column and *Period* either the period before or after the switch from LPS to LED lamps. Since a total bat activity could be strongly driven by species identity (some species can have more weight than other due to their local abundance or their distance of detection), instead of summing the activity of the different species, we thus added a nested random effect on the species to all models with *total number of bat passes* as response variable.

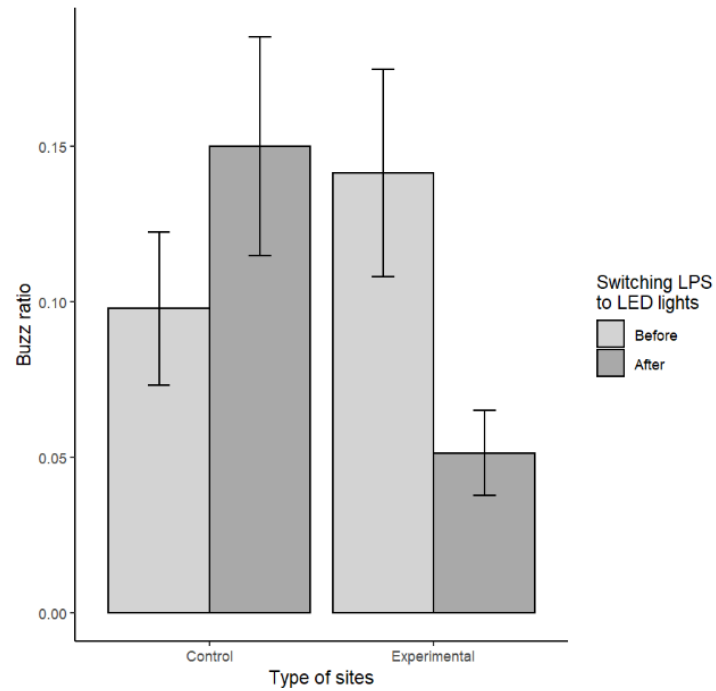
Results concerning BACIP-based analyses, like in Rowse et al. (2016), i.e. when light intensity was not accounted for

We did not find any significant effect of the switch from LPS to LED on the number of bat passes when. However, we found significant effects of the switch-over on the buzz ratio (Table 3). Specifically, we found that at experimental sites the switch from LPS to LED lamps strongly decreased the buzz ratio, while for control site which stayed lit using LPS throughout the study the buzz ratio tended to increase between these periods (Table 3; Figure 4).

Table S1. Estimates, standard errors (SE) and P-value of the bat activity at control (i.e. without change of LPS lights) and experimental sites (i.e. with LPS lights switched to LED lights) before and after LPS lights were switched to LED lights. Here, the ‘reference’ category (i.e. the intercept) is ‘control’ and is identified as a category of comparison for the other categories (here ‘experimental’).

	Estimate ± SE	P-value
<i>Total bat activity</i>		
Intercept	3.815 ± 0.840	<0.001
Experimental vs Control	0.173 ± 0.316	0.584
Before vs after	0.161 ± 0.308	0.600
Experimental vs. Control : before vs. After period	-0.340 ± 0.425	0.425
<i>Pipistrellus pipistrellus</i>		
Intercept	5.977 ± 0.429	<0.001
Experimental vs Control	0.432 ± 0.481	0.369
Before vs after	0.042 ± 0.490	0.932
Experimental vs. Control : before vs. After period	-0.398 ± 0.645	0.537
<i>Pipistrellus pygmaeus</i>		
Intercept	3.674 ± 0.631	<0.001
Experimental vs Control	0.568 ± 0.658	0.388
Before vs after	-1.121 ± 0.643	0.081
Experimental vs. Control : before vs. After period	-0.815 ± 0.832	0.327
<i>Nyctalus spp.</i>		
Intercept	2.490 ± 0.658	<0.001
Experimental vs Control	-0.139 ± 0.553	0.801
Before vs after	0.299 ± 0.587	0.611
Experimental vs. Control : before vs. After period	-0.088 ± 0.757	0.907
<i>Feeding buzz ratio</i>		
Intercept	-1.735 ± 0.141	<0.001
Experimental vs Control	-1.183 ± 0.062	<0.001
Before vs after	-0.487 ± 0.070	<0.001
Experimental vs. Control : before vs. After period	1.601 ± 0.091	<0.001

Figure S2. Predicted buzz ratios of *P. pipistrellus* at control (i.e. lit using LED lamps throughout both years of the experiment) and experimental sites (i.e. lit using LED lamps only the first year and LPS lamps only the second year) before and after the switch from LPS to LED lamps under experimental sites. Results come from the BACIP modelling.



Supplementary Material 4: assessment of the relative importance of environmental variables on bat activity before the experiment of shift from LPS to LED, thus only under LPS streetlight

We assessed the relative importance of environmental variables on bat activities using a Generalized Linear Model (GLM, function `glm`, R package ‘stat’). According to the nature of the response and potential over dispersion of data we performed modeling with a negative binomial (link = log) (Zuur *et al.* 2009), except for the feeding buzz ratio, for which we used a quasi-binomial distribution (link = logit). As some variables were too correlated (i.e. Power and Illuminance) we ran separate regressions to avoid multi-collinearity problem. Thus, our statistical models were structured in the following way:

Bat activity ~ Environmental variable

Where *Bat activity* is either the total activity (*Activity*), the number of buzz (*Buzz*) or the activity of a single species, for *P. pipistrellus*, *P. pygmaeus* or *Nyctalus ssp*; and *Environmental variable* is either the height of the streetlamp (*Height*), the power in watts (*Power*), the illuminance (lux), the distance to a wooded area expressed in meter (*Dist. Wood*), the distance to freshwater expressed in meter (*Dist. Water*) and the distance to grassland expressed in meter (*Dist. Grass*) (the three distance variables being log-transformed).

Table S2. Effect of environmental variables on bat activities (β is the estimate of GLM), P-values were calculated using an ANOVA with a F-test for expressed. According to the need to adjust P-values for multiple comparisons, Bonferroni correction indicates that a $\alpha=0.05$ threshold level should be considered here as $\alpha=0.008$, thus significant P-values in regard to Bonferroni correction are indicated in bold, * indicated that error distribution used was a quasi-poisson instead of a negative binomial due to problem of model convergence.

Power	Illuminance	Height	Dist. Wood	Dist. Water	Dist. Grass
<i>Total Activity</i>					
0.016 ± 0.008	$\beta=0.019 \pm 0.006$	$\beta=0.224 \pm 0.098$	$B=-0.012 \pm 0.006$	$\beta=8.2e-05 \pm 1.1e-03$	$\beta=-0.002 \pm 0.002$
$P=0.045$	$P=0.003$	$P=0.028$	$P=0.040$	$P=0.932$	$P=0.297$
<i>P. pipistrellus</i>					
$\beta=-0.002 \pm 0.009$	$\beta=0.005 \pm 0.007$	$\beta=-0.011 \pm 0.116$	$\beta=-0.009 \pm 0.006$	$\beta=0.001 \pm 0.001$	$\beta=0.001 \pm 0.002$
$P=0.812$	$P=0.567$	$P=0.922$	$P=0.065$	$P=0.144$	$P=0.746$
<i>P. pygmaeus</i>					
$\beta=0.032 \pm 0.011$	$\beta=0.032 \pm 0.009$	$\beta=0.431 \pm 0.127$	$\beta=-0.020 \pm 0.009$	$\beta=0.0004 \pm 0.002$	$\beta=-0.005 \pm 0.003$
$P=0.010$	$P=0.011$	$P=0.004$	$P=0.031$	$P=0.863$	$P=0.132$
<i>Nyctalus ssp.</i>					
$\beta=0.061 \pm 0.015$	$\beta=0.047 \pm 0.010$	$\beta=0.745 \pm 0.1791$	$\beta=-0.020 \pm 0.014$	$\beta=1.313 \pm 0.486$	$\beta=0.881 \pm 0.413$
$P<0.0001$	$P<0.0001$	$P<0.0001$	$P=0.358$	$P=0.008$	$P=0.046$
<i>Feeding buzz ratio</i>					
$\beta=0.012 \pm 0.005$	$\beta=0.008 \pm 0.003$	$\beta=0.1355 \pm 0.061$	$\beta=-0.007 \pm 0.004$	$\beta=-0.001 \pm 0.001$	$\beta=-0.001 \pm 0.001$
$P=0.035$	$P=0.048$	$P=0.044$	$P=0.113$	$P=0.244$	$P=0.585$

In addition to the regression modelling that informed on the significance of each effect one by one, we used the Hierarchical Partition of the variance (R package hier.part) to identify the most likely causal factors while alleviating multicollinearity problems (Mac Nally, 2000).

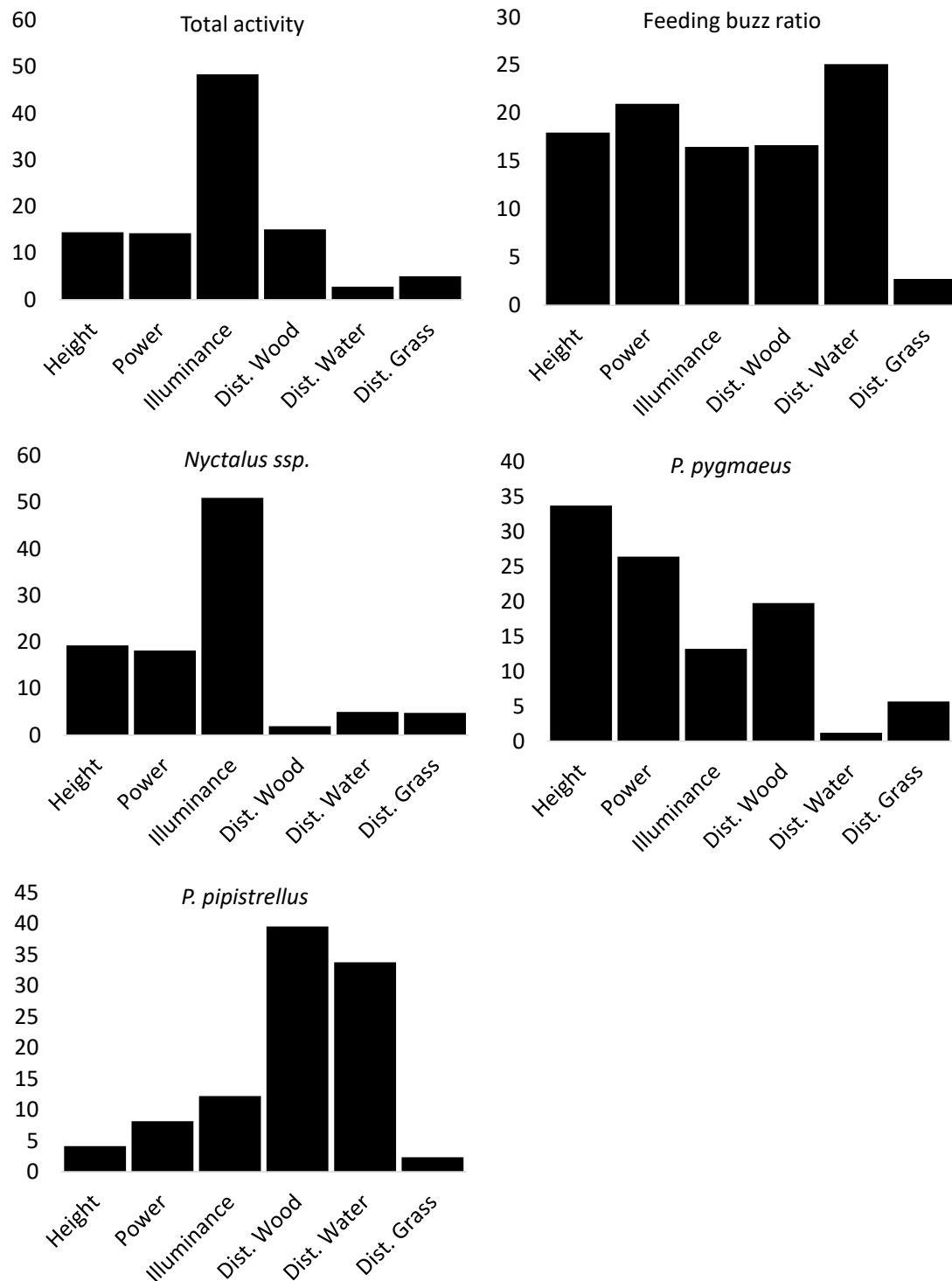


Figure S3: Percentage of total explained variance.

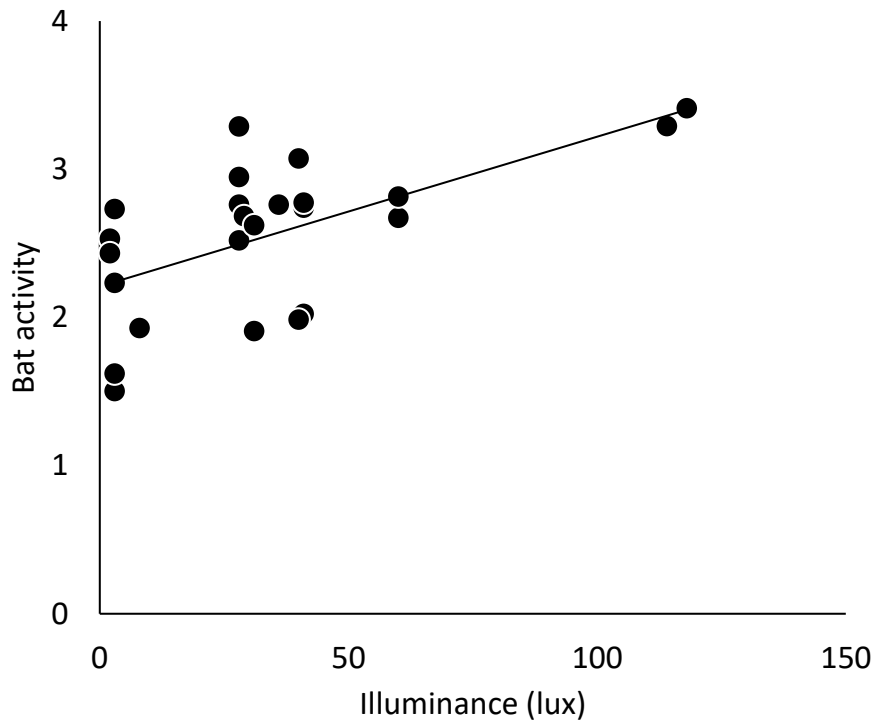


Figure S4. Relationship between bat activity (log-transformed of the number of bat passes) and illuminance (lux) at the 24 LPS streetlights in control and experimental sites before the switch

References

- Mac Nally, R., 2000. Regression and model building in conservation biology: biogeography and ecology: the distinction between and reconciliation of 'predictive' and 'explanatory' models. *Biodiversity and Conservation* 9, 655–671.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R. Springer-Verlag, New York, pp. 322–342.

Appendix V: Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: A call for action

PERSPECTIVE

Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: A call for action

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Abstract

Wind power generation has grown exponentially over the past 20 years to meet international goals of increasing the share of renewables in energy production. Yet, this process has too often been conducted at the cost of airborne biodiversity such as birds and bats. The latter are severely threatened due to deaths by collision at wind turbine. The UNEP/EUROBATS agreement that came into force in 1994 is now ratified by 37 countries; since 2008, it recommends to site wind turbines at least 200 m away from woody edges to decrease bat fatality risks. However, 14 years later we still do not know to what extent this international recommendation has been applied in Europe. We assessed siting distances between woody edges and wind turbines for the largest wind energy producers among the UNEP/EUROBATS parties: the UK, Germany, and France. We show that 61%, 78%, and 56%, respectively, of the installed wind turbines did not comply with UNEP/EUROBATS guidelines, without improvement over time. We identified probable causes of these findings and provided

Kévin Barré and Jérémy S. P. Froidevaux contributed equally as first authors.

The article targets all scientific, technical, and institutional actors involved in the application of the mitigation hierarchy and the environmental impact assessment for wind energy.

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key policy recommendations to achieve compliance to UNEP/EUROBATS guidelines such as better: (i) inclusion in regulatory texts, (ii) notification of the environmental authorities, and (iii) strategic, well-informed, forward planning of areas suitable for wind turbine development.

KEYWORDS

avoidance, bats, collision risk, conservation planning, ecological impact assessment, international environmental agreement, mitigation hierarchy, policy

1 | INTRODUCTION

The join report of IPBES (2021) and IPCC concluded that “Biodiversity loss and climate change are both driven by human economic activities and mutually reinforce each other. Neither will be successfully resolved unless both are tackled together.” In line with international treaties such as the 2016 Paris agreement to reduce global CO₂ emissions, the use of wind turbines to generate electricity (“wind energy”) has grown exponentially over the last 20 years and still represents today the most rapidly expanding form of “renewable energy” worldwide (GWEC, 2021). While wind farm installation has a relatively small footprint on the ground, with little direct loss of habitat, they are not free from negative impacts on biodiversity, particularly for birds and bats, through: (1) mortality events by collision, which can threaten population viability (Frick et al., 2017) and (2) a reduced attractiveness of adjacent habitats (Barré et al., 2018). The challenge of reconciling biodiversity conservation and wind energy production lies in the fact that ecological impacts of wind energy continuously occur throughout the operational phase (i.e., usually more than 20 years), and it is still difficult to accurately predict impacts prior to installation (Katzner et al., 2019). To deal with such impacts, wind energy developers must apply the mitigation hierarchy, which is a well-established framework to counteract impacts of development projects by avoiding (i.e., avoid spatial locations where high impact is expected), reducing (e.g., decreasing wind turbine cut-in speed to reduce collision risks) and as a last resort, offsetting the biodiversity losses (e.g., creation of new habitats; BBOP, 2012; Gardner et al., 2013). Furthermore, when impacts are correctly identified, application of the legal mitigation hierarchy does not always avert the risk (Lintott et al., 2016). Indeed, reduction strategies such as curtailment of wind turbines under bat-friendly weather conditions have a variable and never total efficiency (Adams et al., 2021; Whitby

et al., 2021), suggesting that the avoidance stage of the mitigation hierarchy should be preferred to reduction and offsetting strategies (Phalan et al., 2018).

The avoidance strategy constitutes a key recommendation from the Agreement on the Conservation of Populations of European Bats (UNEP/EUROBATS) set up under the Convention on the Conservation of Migratory Species of Wild Animals. Bats are covered by the Habitats Directive of the European Union (92/43/EEC), and thus strictly protected in member countries who must adopt measures to avoid impacts on populations of this taxon being highly sensitive to wind turbines. UNEP/EUROBATS published its first resolution on *Wind Turbines and Bat Populations* in 2003 (Resolution 4.7) mentioning the need for an environmental impact assessment prior to selecting appropriate construction sites. This resolution was replaced by a revision in 2006 (Resolution 5.6), which contained the first generic *Guidelines for the planning process and impact assessments* recommending to install wind turbines more than 200 m away from any woody edges (i.e., forests and hedgerows) to reduce bat fatality risk in Europe (Rodrigues et al., 2006). Subsequent resolutions followed and detailed guidelines were published in 2008 and updated in 2014, still including the 200 m buffer rule (Rodrigues et al., 2015). Indeed, woody edges constitute a key foraging and commuting habitat for many bat species (Boughey et al., 2011; Froidevaux et al., 2019; Verboom & Huitema, 1997). Although there is still no evaluation of the effect of modifying wind turbine distance to woody edges on the reduction of bat fatality risk (Berthinussen et al., 2021), the EUROBATS guideline was evidently based on the best available science and formulated as a precautionary principle. Moreover, three studies show that the increase of tree cover around wind turbines and the distance to woody habitats are ones of the main factors of collision risks in Europe (Roemer et al., 2019; Rydell et al., 2010; Santos et al., 2013). In addition, a recent study highlighted that wind turbines no longer attract bats beyond a distance of at least about a 100 m

from woody edges (Leroux et al., 2022). None of these studies have proposed an optimal distance for siting wind turbines from woody edges, but many other studies demonstrated that bat activity, although not a direct reflection of the collision risk, decreases with increasing distances to woody edges, and that activity levels at 200 m from woody edges are very low for most bat species (e.g., Heim et al., 2017; Kelm et al., 2014).

The UNEP/EUROBATS agreement has been ratified by 37 countries, which shall adopt and enforce required legislative and administrative measures in order to implement the recommended guidelines. Yet, a recent synthesis underlines that practice could fail to adopt recommendations despite clear research and evidence (Hunter et al., 2021). So, after almost 20 years after the first resolution and almost 14 years since the publication of the first edition of the guidelines in many European languages, we still do not know how the UNEP/EUROBATS recommendations on wind turbine siting are applied in Europe. First results from Barré et al. (2018) showed that in a French region with high hedgerow density, 89% of wind turbines installed after 2008 were sited at <200 m from woody edges, but no study to date has carried out this assessment on a broad scale. Thus, given that the population viability of bats is highly sensitive to losses of individuals through collision with wind turbines (Frick et al., 2017; Friedenberg & Frick, 2021), a large-scale assessment of wind turbine siting in relation to woody edges is of crucial importance.

Here, we assess the compliance with the UNEP/EUROBATS guideline of siting wind turbines at least 200 m away from woody edges. We make this assessment for the three largest wind energy contributors among the signatory members of the UNEP/EUROBATS agreement representing together 47% of the total installed capacity in Europe (GWEC, 2021): the UK, Germany, and France, which have each ratified UNEP/EUROBATS in 1992, 1993, and 1995, respectively. We then identify the probable causes of the findings and provide key policy recommendations that could be easily implemented in the near future to comply with the UNEP/EUROBATS guidelines.

2 | METHODS FOR ASSESSING COMPLIANCE OF WIND ENERGY CONTRIBUTORS WITH THE UNEP/EUROBATS GUIDELINE

To evaluate the application of the UNEP/EUROBATS guideline of siting wind turbines at least 200 m away from woody edges at a broad spatial scale, we computed the distance of wind turbines to the nearest woody edge in the UK, Germany, and France. We adopted different methodological approaches between countries. In the UK and Germany, the lack of available national-scale high-

resolution land-cover or hedgerow data led us to manually measure distances between wind turbines and woody edges using satellite imagery. Thus, we created a random subset of wind turbines (~1000 wind turbines per country) using QGIS v.3.18.3 coupled with Google Satellite Imagery (see Supporting Information 1 for more details). In France, we used high-resolution land-cover data (CES OSO, <http://osr-cesbio.ups-tlse.fr/oso/>, 10 m resolution) and data from the French National Bocage Monitoring System (IGN, BD Haie, <https://geoservices.ign.fr/>) to map forest cover and hedgerows at the national scale, respectively. We then automatically computed the Euclidean distance between each of the 8066 wind turbines installed until 2020 and the nearest forest patch or hedgerow using automated distance computations (see Supporting Information 1 for more details). Furthermore, as the computation of distances between wind turbines and woody edges was done manually for the UK and Germany, and automatically for France, we could only consider the period 2009–2020 (i.e., period starting 1 year following the publication of the UNEP/EUROBATS guidelines) for the formers; whereas, we could focus on the whole period (1991–2020) for the latter.

Then, based on these computations we assessed at the national scale the cumulated number of wind turbines in relation with the distance to the nearest woody edge in the UK, Germany, and France, for the period after the publication of the recommendations (i.e., 2009–2020). Since we had access to a more detailed dataset in France, we also assessed this compliance for each administrative region and for the periods prior to (1991–2008) and after (2009–2020) the initial UNEP/EUROBATS guidelines publication in 2008.

Finally, thanks to the exhaustive dataset in France, we assessed whether changes in wind turbines siting occurred in France after the publication of the European guidelines in 2008. We performed generalized linear mixed-effects models (GLMMs, “glmmTMB” R-package; Brooks et al., 2017) with a negative binomial distribution to handle right-skewed and long-tailed distribution and overdispersion. Wind turbine distance from woody edges was included as a response variable while year of wind turbine construction and its quadratic term to detect possible nonlinear relationship were considered as fixed effects. We conducted GLMMs at both national and regional scales, considering only regions for which sufficient information on the year of wind turbine construction was available (i.e., Bourgogne-Franche-Comté, Bretagne, Centre-Val de Loire, Hauts-de-France, Occitanie, and Pays de la Loire; Table 1). To account for within region and wind farm dependency in the measurements, we included wind farm identifier nested within region identifier as random effects into the model performed at the national scale, and wind farm identifier alone as random effect for models at the regional scale. Given that residuals of most models were spatially

TABLE 1 Summary for France at national and regional scales, and for Germany and UK at national scale, of the total number of wind turbines, the number of wind turbines with a known construction date, the proportion of wind turbines at <200 m from the nearest woody edge for all years, before and after UNEP/EUROBATS guidelines publication

Country	Scale	Number of wind turbines	Number of known wind turbines siting date	Proportion of wind turbines at <200 m from woody edges		
				All years	Before 2008 Eurobats guidelines	After 2008 Eurobats guidelines
Germany	National scale	984 (subset)	984	/	/	0.78
UK	National scale	818 (subset)	818	/	/	0.61
France	National scale	8066	4658	0.58	0.62	0.56
	Auvergne-Rhone-Alpes region	354	5	0.90	/	1.00
	Bourgogne-Franche-Comté region	390	345	0.74	0.95	0.70
	Bretagne region	618	609	0.99	1.00	0.99
	Centre-Val-de-Loire region	503	503	0.23	0.18	0.25
	Corse region	30	30	1.00	1.00	/
	Grand-Est region	1654	0	0.42	NA	NA
	Hauts-de-France region	1971	1764	0.33	0.37	0.32
	Ile-de-France region	43	0	0.19	NA	NA
	Normandie region	529	0	0.57	NA	NA
	Nouvelle-Aquitaine region	533	0	0.87	NA	NA
	Occitanie region	855	820	0.81	0.73	0.85
	Provence-Alpes-Côte d'Azur region	68	68	0.44	0.21	0.66
	Pays-de-la-Loire region	518	514	0.82	0.83	0.82

Note: Since Germany and the UK were studied using subsets of randomly selected wind turbines operating after 2009, the proportion of wind turbines at <200 m from woody edges is only provided for the post-publication period of the UNEP/EUROBATS guidelines.

autocorrelated (Moran's *I* test, *p*-value <.05), we also added a spatial autocovariate as a fixed effect in these models. When including this variable, Moran's *I* test was no longer significant (*p*-value >.05) (see Supporting Information 2 for more details).

3 | THE THREE LARGEST WIND ENERGY CONTRIBUTORS DO NOT COMPLY WITH THE UNEP/EUROBATS GUIDELINE

Our results show that after the publication of the UNEP/EUROBATS guidelines in 2008, 61%, 78%, and 56% of the wind turbines from the UK, Germany, and France, respectively, have been installed at <200 m distance from woody edges and thus do not comply with the guideline (Figure 1; Table 1). In all three countries, wind turbines were installed even within forests, after the publication of UNEP/EUROBATS guidelines (3% of the wind turbines in UK, 13% in Germany, and 3% in France). Over the whole period, the proportion of wind turbines installed at <200 m from woody edges varied from 19% to 90% according to the

French region considered (Figure 2; Table 1), and was very similar between the two woody edge types (i.e., hedgerows and forest edges; Figure 2). Siting distances from woody edges did not substantially improve over time in France, since the proportion of wind turbines installed at <200 m from woody edges only decreased from 62% to 56% between the periods before and after 2008 (Table 1), and did not improve locally either (Figure 3; Table 2 and Supporting Information S2). The proportion of wind turbines, which failed to comply with the guideline since their publication in 2008 varied from 25% to 100% according to the French region considered (Table 1). Our temporal analysis did not include three regions with large wind energy capacity because construction dates were not publicly available (despite the 2003/4/CE directive on public access to environmental information), namely Grand-Est, Normandie, and Nouvelle-Aquitaine, which have proportion of wind turbines installed at <200 m from woody edges of 42%, 57%, and 87%, respectively (Table 1). While we acknowledge that some wind turbines installed in 2009 and 2010 in the three countries may result from construction authorizations given prior to the publication of the guidelines (2008), this is very unlikely to bias the results given that (i) the

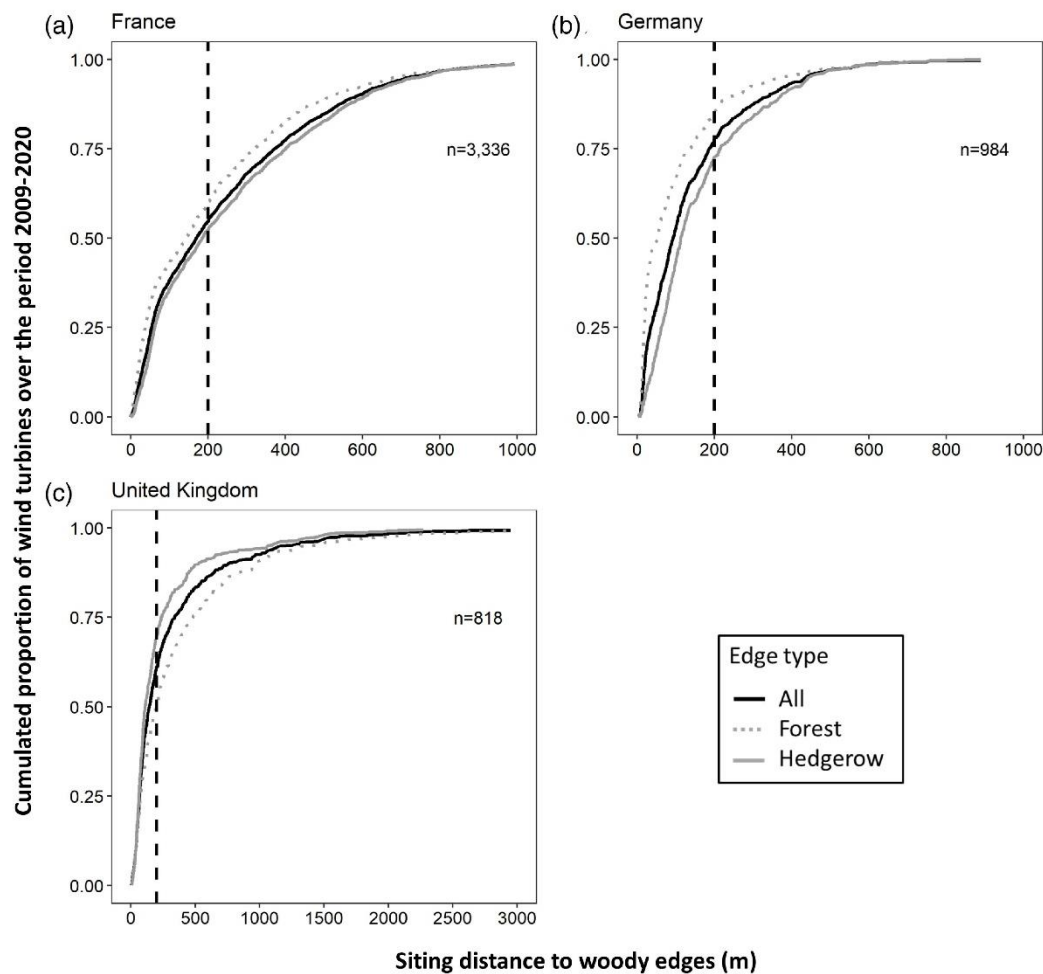


FIGURE 1 Cumulated proportion of wind turbines in operation since 2009 in relation with siting distance to woody edges in (a) France, (b) Germany, and (c) UK. Vertical black dashed lines represent the minimum distance of wind turbine siting to woody edges from UNEP/EUROBATS guidelines (i.e., 200 m)

proportion of wind turbines included in these years corresponds to a small fraction of the total wind turbines over the 2009–2020 period (i.e., 11%) and (ii) the percentage of wind turbines at <200 m from woody edges remains very high (i.e., from 31% to 63% and 44% in average) each year between 2009 and 2020 (Table S3).

4 | PROBABLE CAUSES OF SITING WIND TURBINES NEAR WOODY EDGES

4.1 | Absence of implementation of the UNEP/EUROBATS guideline in national laws

UNEP/EUROBATS is an international environmental agreement acceded by 37 states and binds its states

parties on the conservation of bats in their territories. However, to be effective, parties of the UNEP/EUROBATS agreement “shall adopt and enforce such legislative and administrative measures as may be necessary for the purpose of giving effect to this Agreement” and “The provisions of this Agreement shall in no way affect the right of Parties to adopt stricter measures concerning the conservation of bats” (*article IV of the Agreement on the Conservation of Bats in Europe, London, 1991*). Like in the case of many other agreements, it is thus up to member states to create adequate legislative measures, but not doing so is unlikely to result in major consequences for these states. The failure of member countries to apply the international environmental agreements that they have ratified has been diagnosed repetitively (Kellenberg & Levinson, 2014; Ringquist & Kostadinova, 2005). Although the mitigation hierarchy for wind energy projects is implemented in the British,

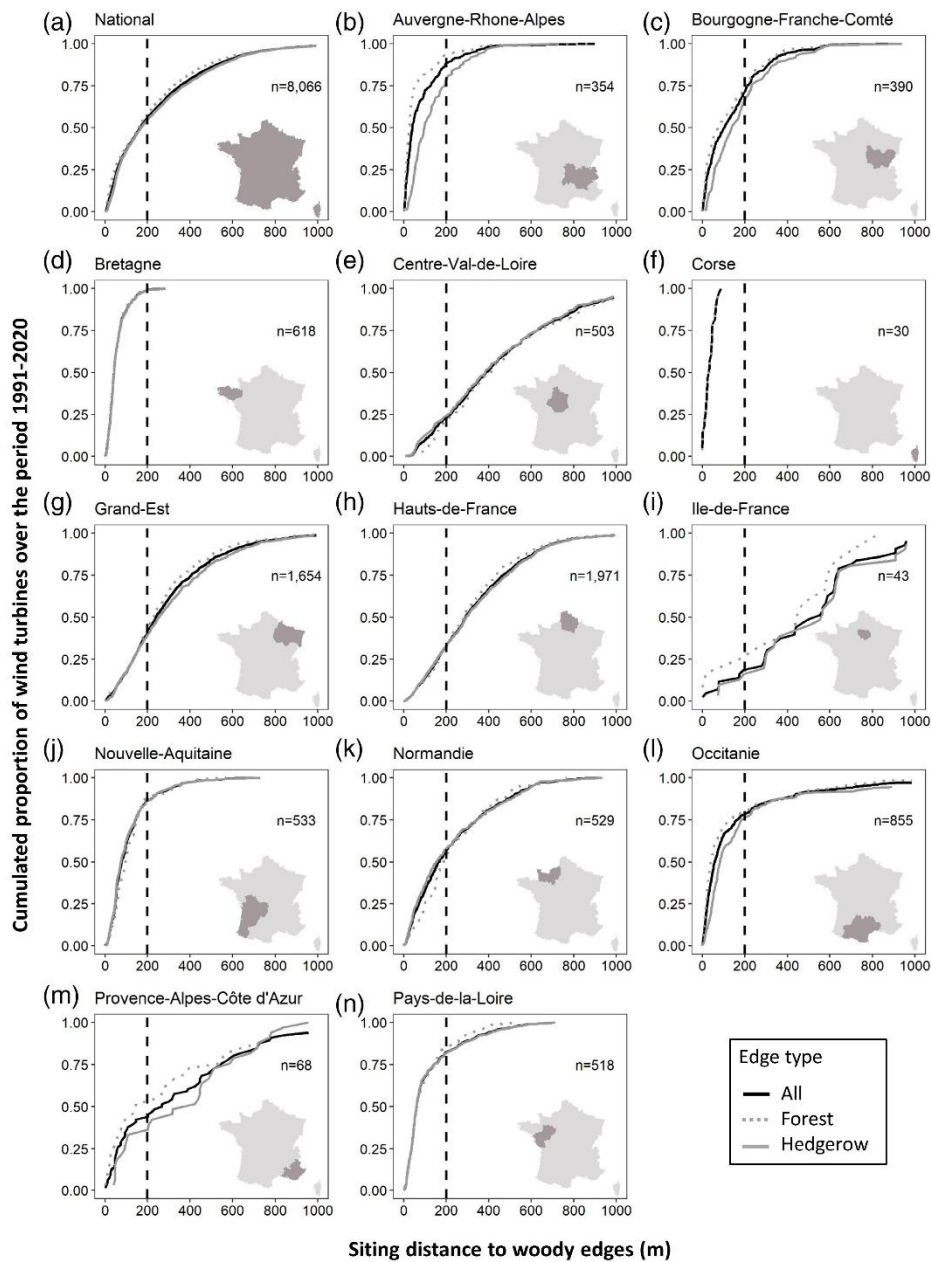


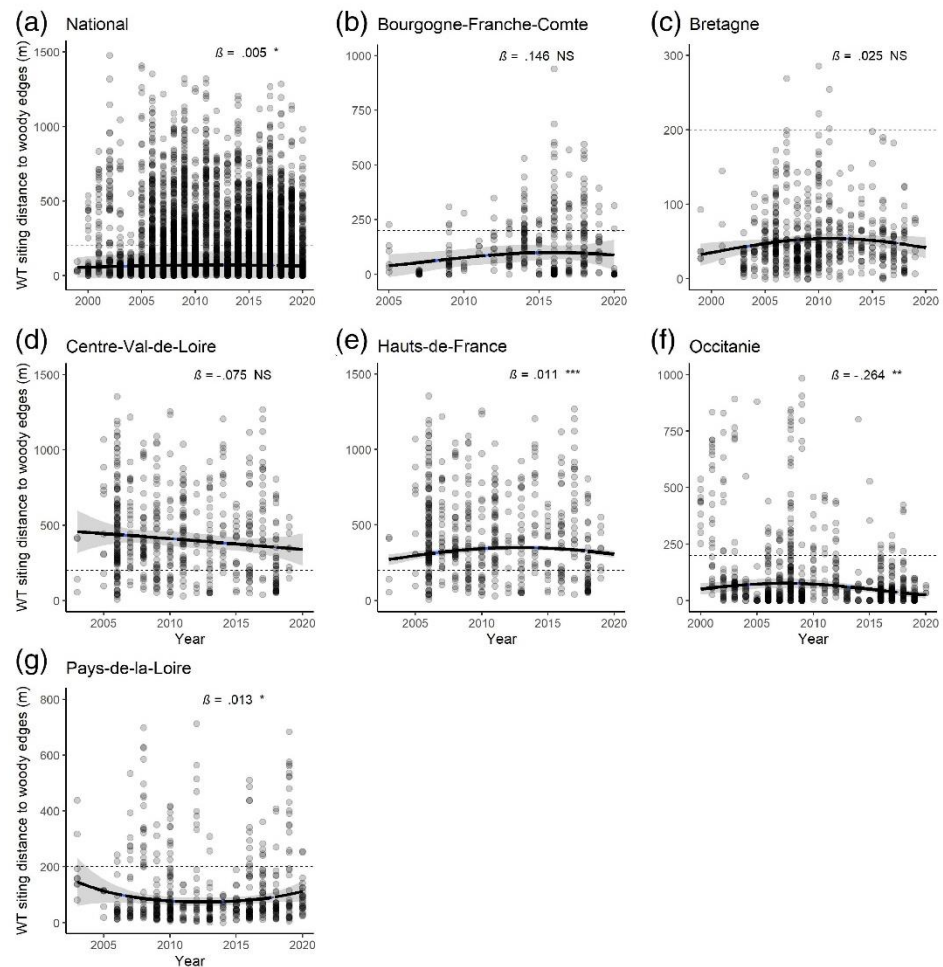
FIGURE 2 Cumulated proportion of French wind turbines in operation over the whole period (1991–2020) in relation with siting distance to woody edges at (a) national and (b–n) regional scales. Vertical black dashed lines represent the minimum distance of wind turbine siting to woody edges from UNEP/EUROBATS guidelines (i.e., 200 m)

German, and French legislative frameworks, it is not the case of the key recommendation of UNEP/EUROBATS (i.e., avoid siting wind turbines near woody edges).

To practically guide stakeholders during the environmental impact assessment of wind energy projects, the mitigation hierarchy framework was translated into national or federal guidance. The British guidance on *bats and onshore wind turbines—survey, assessment and mitigation* (NatureScot et al., 2021) mentions the UNEP/EUROBATS guidelines but argues that a 50 m buffer around woodland areas is adequate in most, lower risk situations. It is very likely then that the national guidance

takes precedence over the UNEP/EUROBATS guideline. We found that 15% of the wind turbines from the UK have been installed at <50 m from woody edges. The French *guidance to the preparation of impact studies for onshore wind farm projects* (Ministère de la Transition Ecologique, 2020) simply mentions the existence of the UNEP/EUROBATS guidelines and specifies that they are not mandatory; it also states that in the case of non-respect, the absence of impacts of bats must be demonstrated. However, the French guidance does not explicitly mention the 200 m distance to woody edges recommended by UNEP/EUROBATS and does not remind the

FIGURE 3 French wind turbine siting distance to woody edges as a function of the year at (a) national and (b–g) regional scales. Solid black lines represent the predictions from GLMMs with gray areas corresponding to 95% confidence intervals around the predictions. Horizontal dotted lines represent the minimum distance of wind turbine siting to woody edges from UNEP/EUROBATS guidelines (i.e., 200 m). β parameters and significance level ($***p < .001$, $**p < .01$, $*p < .05$, NS, non-significant with $p \geq .05$) are annotated on each figure



ecological grounds for this distance and why it is important to consider it seriously. Thus, this regulatory text is probably encouraging not to follow the guidelines. Similarly, in Germany, where guidance exist for each of the 16 federal states; a minority recommends to install wind turbines at more than 200 m from woody edges (Hurst et al., 2015) and in current discussions about spatial planning regulations (e.g., guidance updates), there is strong political willing to even decrease setback distances and increase the number of wind turbines within forests (Bunzel et al., 2019). It is therefore unlikely that Germany will comply with the UNEP/EUROBATS distance recommendations in the future.

4.2 | Lack of knowledge, training, and capacity in environmental authorities

Since the content of the guidelines is not written in national and/or federal regulatory texts, it is likely that staff from environmental permitting and regulatory

authorities assessing the admissibility of environmental impact assessment studies are simply not aware of their precise content. In addition, decision makers can lack both competence and capacity to use scientific literature to inform their decisions, although UNEP/EUROBATS guidelines were disseminated and translated in many languages, and this remains a common issue in conservation (Downey et al., 2021).

4.3 | Landscape structure

Siting decisions are quite often driven by financial or political interests rather than based on evidence-based conservation issues (Burke & Stephens, 2018). Indeed, to set up a wind farm, promoters are first legally required to avoid all exclusion zones (e.g., roads, high power lines, aviation, military zones, urban areas, and wind farms; Staid & Guikema, 2013). Once all of these constraints are avoided, keeping wind turbines at more than 200 m away from any woody edges adds a strong constraint, although

TABLE 2 Estimated parameters, standard errors (SE) and *p*-values of the effect of the year, the quadratic year and the “autocov” covariate (accounting for spatial autocorrelation) on the wind turbine siting distance to woody edges from GLMMs at national and regional scales in France

Variables	National scale			Bourgogne-Franche-Comté			Bretagne			Centre-Val de Loire			Hauts-de-France			Occitanie			Pays de la Loire		
	$\beta \pm SE$	<i>p</i>		$\beta \pm SE$	<i>p</i>		$\beta \pm SE$	<i>p</i>		$\beta \pm SE$	<i>p</i>		$\beta \pm SE$	<i>p</i>		$\beta \pm SE$	<i>p</i>		$\beta \pm SE$	<i>p</i>	
Intercept	4.22 ± 0.65	<.001		4.51 ± 0.141	<.001		3.92 ± 0.04	<.001		6.00 ± 0.04	<.001		5.80 ± 0.02	<.001		4.02 ± 0.11	<.001		4.45 ± 0.07	<.001	
Year	33.86 ± 14.81	.022		108.98 ± 135.37	.421		58.90 ± 32.41	.070		4.09 ± 43.14	.924		49.84 ± 14.80	<.001		168.41 ± 58.20	.004		-134.16 ± 62.43	.032	
Year ²	-33.85 ± 14.80	.022		-108.84 ± 135.37	.421		-58.87 ± 32.41	.070		-4.17 ± 43.14	.923		-49.83 ± 14.80	<.001		-168.67 ± 58.24	.004		134.17 ± 62.43	.032	
Autocov	0.02 ± 0.01	.102		0.51 ± 0.10	<.001		-	-		0.32 ± 0.03	<.001		0.03 ± 0.02	.129		0.27 ± 0.03	<.001		-	-	

avoiding impacts on biodiversity is also a legal requirement. For instance, according to our findings, 99% of wind turbines of the Bretagne region in France (area with high hedgerow density: 63.24 m/ha) were not installed following the UNEP/EUROBATS guideline; in comparison, 25% of turbines were not installed following the UNEP/EUROBATS guideline in the Centre-Val-de-Loire region (area with low hedgerow density: 23.74 m/ha).

In addition, local ecological impacts are only considered in a very late planning stage (i.e., during the environmental impact assessment) once a very limited potential siting area has been defined, which strongly limits the possibilities of impact avoidance (Phalan et al., 2018), and leads stakeholders to quickly switch to reduction measures. However, reduction measures are not necessarily fully effective, whether it be short-distance deterrence (Gilmour et al., 2020) or cut-in speed (Adams et al., 2021; Whitby et al., 2021) strategies. This stresses the crucial need of prioritizing avoidance strategies such as this UNEP/EUROBATS guideline before considering reduction strategies.

5 | RECOMMENDATIONS FOR SITING FUTURE WIND TURBINES AWAY FROM WOODY EDGES

To comply with the UNEP/EUROBATS agreement and meet the associated goals of bat conservation, we thus recommend that (1) member states should urgently work on the implementation of the UNEP/EUROBATS recommendations—notably concerning the siting of wind turbines—in their legislative framework, and (2) national and regional guidance should be updated to explicitly mention recommendations made in UNEP/EUROBATS guidelines and actively encourage their application to provide more detailed guidance for stakeholders. We further recommend that (3) environmental permitting and regulatory authorities should invest in the scientific training of their staff and ensure that staff with ecological expertise have the capacity, competence and influence that is necessary to guarantee that their decisions will be evidence-based and will follow national and international guidelines for bat conservation. In parallel, scientific research could also be intensified on the relationship between collision risk and distance to woody edges according to biogeographic and landscape context. Of course, this uncertainty should in no way justify the non-compliance with the current guideline. Our last recommendation is that (4) ecological impacts should be considered right at the beginning of the planning process—in a strategic way, long before individual planning applications are submitted, when all options are still available—to efficiently avoid impacts of

wind turbines. To promote this process, guidance should place wind turbine siting distances from woody edges, and by extension the distance of tree planting siting to wind turbines, at the core of the avoidance strategies, even before defining the potential siting area. Creating maps on which areas at more than 200 m from woody edges (i.e., forests and hedgerows) are highlighted will help environmental permitting and regulatory authorities sort out impact assessment studies that do not comply with the UNEP/EUROBATS guideline. Beyond better anticipation of siting distances from woody edges, other aspects should also be increasingly considered for impact avoidance such as the migration routes for bats, and more generally the probability of species presence considering ecologically relevant habitat variables (Voigt et al., 2016). Species distribution modeling frameworks could be developed at regional, national or continental scales to identify areas where siting wind turbines should be avoided, following examples in the USA (Wieringa et al., 2021), Scotland (Newson et al., 2017), or Italy (Roscioni et al., 2013).

6 | CONCLUSION

Our argument shows that solutions exist to improve the currently insufficient levels of compliance with the UNEP/EUROBATS guideline. However, addressing these solutions (e.g., the lack of anticipation in wind turbine planning) may not be sufficient in specific cases, especially in landscapes with high woody edge density. We therefore also call for states to rethink their strategies regarding the spatial allocation of renewable energy production in their territories, and ask themselves this question: is it reasonable for all areas of a given country to produce a similar amount of wind energy? This strategy can indeed be explained by the will of states to guarantee equality in the access to renewables to all administrative regions. Still, it is possible to guarantee this access by choosing a type of renewable energy that is compatible with the landscape composition; for instance, by prioritizing the installation of wind turbines in open fields and by prioritizing the installation of solar panels on rooftops in areas with high woody edge densities. A local production of energy should in any case be recommendable (Koirala et al., 2016). A better compliance with the UNEP/EUROBATS guideline may also not be sufficient for migrating bats for which woody features are poor predictors of collision risks (Roemer et al., 2019). In this case other measures may be necessary to reduce bat fatalities, such as wind turbine curtailment strategies based on weather, date and time (Behr et al., 2017). Finally, it is now well established that energy consumption is disproportionately increasing compared to population growth,

and that this trend is a threat for our future well-being (Pasten & Santamarina, 2012). We thus relay the recommendations of the IPBES and the IPCC to reduce our consumption and production of energy to avoid the need to install more wind turbines on an area than biodiversity can cope with.

AUTHOR CONTRIBUTIONS

Conceived the idea: Kévin Barré, Jérémy S.P. Froidevaux, and Charlotte Roemer. *Collected data for France and the UK:* Kévin Barré, Jérémy S.P. Froidevaux, and Charlotte Roemer. *Performed analyses:* Kévin Barré, Jérémy S.P. Froidevaux, and Charlotte Roemer. *Led writing of the manuscript:* Kévin Barré, Jérémy S.P. Froidevaux, and Charlotte Roemer. *Computed distances between wind turbine and woody edges:* Kévin Barré, Jérémy S.P. Froidevaux, Charlotte Roemer, Camille Leroux, and Léa Mariton. *Collected shapefile data for Germany:* Marcus Fritze. All authors contributed to the preparation of the manuscript, and approved the final version for submission.

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CONFLICT OF INTEREST

Auddicé biodiversité is an environmental consultancy involved in wind turbine impact assessment studies, and funded the author Camille Leroux at the time of submission. Camille Leroux thus declare a conflict of interest. The funder had no role in data preparation and analysis, interpretation, and discussion of the results, and decision to publish. Authors take complete responsibility for the accuracy of their analysis and their interpretation and discussion. They declare having no other competing interest.

DATA AVAILABILITY STATEMENT

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REFERENCES

- Adams, E. M., Gulka, J., & Williams, K. A. (2021). A review of the effectiveness of operational curtailment for reducing bat fatalities at terrestrial wind farms in North America. *PLoS One*, 16, e0256382. <https://doi.org/10.1371/journal.pone.0256382>
- Barré, K., Le Viol, I., Bas, Y., Julliard, R., & Kerbiriou, C. (2018). Estimating habitat loss due to wind turbine avoidance by bats: Implications for European siting guidance. *Biological Conservation*, 226, 205–214. <https://doi.org/10.1016/j.biocon.2018.07.011>
- Behr, O., Brinkmann, R., Hochradel, K., Mages, J., Korner-nievergelt, F., Niermann, I., Reich, M., Simon, R., Weber, N., & Nagy, M. (2017). Mitigating bat mortality with turbine-specific curtailment algorithms: A model based approach. In J. Köppel (Ed.), *Wind energy and wildlife interaction. Presentations from the CWW2015 Conference*. 1. Aufl. 1 Band. (pp. 135–160). Berlin, Germany: Springer.
- Berthoussen, A., Richardson, O. C., & Altringham, J. D. (2021). *Bat conservation: Global evidence for the effects of interventions. Conservation evidence series synopses*. University of Cambridge.
- Business and Biodiversity Offsets Programme (BBOP). (2012). *Standard on biodiversity offset*. BBOP.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, 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>
- Burke, M. J., & Stephens, J. C. (2018). Political power and renewable energy futures: A critical review. *Energy Research and Social Science*, 35, 78–93. <https://doi.org/10.1016/j.erss.2017.10.018>
- Boughey, K. L., Lake, I. R., Haysom, K. A., & Dolman, P. M. (2011). Improving the biodiversity benefits of hedgerows: How physical characteristics and the proximity of foraging habitat affect the use of linear features by bats. *Biological Conservation*, 144, 1790–1798. <https://doi.org/10.1016/j.biocon.2011.02.017>
- Downey, H., Amano, T., Cadotte, M., Cook, C. N., Cooke, S. J., Haddaway, N. R., Jones, J. P., Littlewood, N., Walsh, J. C., & Abrahams, M. I. (2021). Training future generations to deliver evidence-based conservation and ecosystem management. *Ecological Solutions and Evidence*, 2, e12032. <https://doi.org/10.1002/2688-8319.12032>
- Frick, W. F., Baerwald, E. F., Pollock, J. F., Barclay, R. M. R., Szymanski, J. A., Weller, T. J., Russell, A. L., Loeb, S. C., Medellín, R. A., & McGuire, L. P. (2017). Fatalities at wind turbines may threaten population viability of a migratory bat. *Biological Conservation*, 209, 172–177. <https://doi.org/10.1016/j.biocon.2017.02.023>
- Friedenberg, N. A., & Frick, W. F. (2021). Assessing fatality minimization for hoary bats amid continued wind energy development. *Biological Conservation*, 262, 109309. <https://doi.org/10.1016/j.biocon.2021.109309>
- Froidevaux, J. S. P., Boughey, K. L., Hawkins, C. L., Broyles, M., & Jones, G. (2019). Managing hedgerows for nocturnal wildlife: Do bats and their insect prey benefit from targeted Agri-environment schemes? *Journal of Applied Ecology*, 56, 1610–1623. <https://doi.org/10.1111/1365-2664.13412>
- Gardner, T. A., Von Hase, A., Brownlie, S., Ekstrom, J. M. M., Pilgrim, J. D., Savy, C. E., Stephens, R. T. T., Treweek, J., Ussher, G. T., Ward, G., & Ten Kate, K. (2013). Biodiversity offsets and the challenge of achieving no net loss. *Conservation Biology*, 27, 1254–1264. <https://doi.org/10.1111/cobi.12118>
- Gilmour, L. R. V., Holderied, M. W., Pickering, S. P. C., & Jones, G. (2020). Comparing acoustic and radar deterrence methods as mitigation measures to reduce human-bat impacts and conservation conflicts. *PLoS One*, 15, 1–16. <https://doi.org/10.1371/journal.pone.0228668>
- GWEC. (2021). *Global wind report 2021*. GWEC. <https://doi.org/10.1542/pir.2019-0271>
- Heim, O., Lenski, J., Schulze, J., Jung, K., Kramer-Schadt, S., Eccard, J. A., & Voigt, C. C. (2017). The relevance of vegetation structures and small water bodies for bats foraging above farmland. *Basic and Applied Ecology*, 27, 1–11. <https://doi.org/10.1016/j.baae.2017.12.001>
- Hunter, S. B., zu Ermgassen, S. O. S. E., Downey, H., Griffiths, R. A., & Howe, C. (2021). Evidence shortfalls in the recommendations and guidance underpinning ecological mitigation for infrastructure developments. *Ecological Solutions and Evidence*, 2, 1–14. <https://doi.org/10.1002/2688-8319.12089>
- Hurst, J., Balzer, S., Biedermann, M., Dietz, C., Dietz, M., Höhne, E., Karst, I., Petermann, R., Schorch, W., Steck, C., & Brinkmann, R. (2015). Erfassungsstandards für Fledermäuse bei Windkraftprojekten in Wäldern. Diskussion aktueller Empfehlungen der Bundesländer. *Natur und Landschaft*, 90, 157–169.
- IPBES. (2021). *Tackling biodiversity & climate crises together and their combined social impacts*. IPBES.
- Bunzel, K., Bovet, J., Thrän, D., & Eichhorn, M. (2019). Hidden outlaws in the forest? A legal and spatial analysis of onshore wind energy in Germany. *Energy Research & Social Science*, 55, 14–25. <https://doi.org/10.1016/j.erss.2019.04.009>
- Katzner, T. E., David, M. N., Jay, E. D., Adam, E. D., Caitlin, J. C., Douglas, L., Hannah, B. V. Z., Julie, L. Y., Maitreyi, S., Manuela, M. P. H., Melissa, A. B., Michael, L. M., Scott, R. L., Sharon, A. P., Tara, J. C., & Miller, T. A. (2019). Wind energy: A human challenge. *Science*, 366, 1206–1207. <https://doi.org/10.1126/science.aaz9989>
- Kellenberg, D., & Levinson, A. (2014). Waste of effort? International environmental agreements. *Journal of the Association of Environmental and Resource Economists*, 1, 135–169. <https://doi.org/10.3386/w19533>
- Kelm, D. H., Lenski, J., Kelm, V., Toelch, U., & Dziock, F. (2014). Seasonal bat activity in relation to distance to hedgerows in an agricultural landscape in Central Europe and implications for wind energy development. *Acta Chiropterologica*, 16, 65–73. <https://doi.org/10.3161/150811014X683273>
- Koirala, B. P., Koliou, E., Friege, J., Hakvoort, R. A., & Herder, P. M. (2016). Energetic communities for community

- energy: A review of key issues and trends shaping integrated community energy systems. *Renewable and Sustainable Energy*, 56, 722–744. <https://doi.org/10.1016/j.rser.2015.11.080>
- Leroux, C., Kerbiriou, C., Le Viol, I., Valet, N., & Barré, K. (2022). Distance to hedgerows drives local repulsion and attraction of wind turbines on bats: Implications for spatial siting. *Journal of Applied Ecology*, 59, 2142–2153. <https://doi.org/10.1111/1365-2664.14227>
- Lintott, P. R., Richardson, S. M., Hosken, D. J., Fensome, S. A., & Mathews, F. (2016). Ecological impact assessments fail to reduce risk of bat casualties at wind farms. *Current Biology*, 26, R1135–R1136. <https://doi.org/10.1016/j.cub.2016.10.003>
- Ministère de la Transition Écologique. (2020). *Guide relatif à l'élaboration des études d'impacts des projets de parcs éoliens terrestres - version révisée octobre 2020*. Ministère de la Transition Écologique.
- NatureScot (Scottish Natural Heritage), Natural England, Natural Resources Wales, RenewableUK, Scottish Power Renewables, Ecotricity Ltd, University of Exeter, Bat Conservation Trust (BCT). (2021). *Bats and onshore wind turbines - survey, assessment and mitigation*. NatureScot (Scottish Natural Heritage). <https://doi.org/10.1542/pir.2019-0271>
- Newson, S. E., Evans, H. E., Gillings, S., Jarrett, D., Raynor, R., & Wilson, M. W. (2017). Large-scale citizen science improves assessment of risk posed by wind farms to bats in southern Scotland. *Biological Conservation*, 215, 61–71. <https://doi.org/10.1016/j.biocon.2017.09.004>
- Pasten, C., & Santamarina, J. C. (2012). Energy and quality of life. *Energy Policy*, 49, 468–476. <https://doi.org/10.1016/j.enpol.2012.06.051>
- Phalan, B., Hayes, G., Brooks, S., Marsh, D., Howard, P., Costelloe, B., Vira, B., Kowalska, A., & Whitaker, S. (2018). Avoiding impacts on biodiversity through strengthening the first stage of the mitigation hierarchy. *Oryx*, 52, 316–324. <https://doi.org/10.1017/S0030605316001034>
- Ringquist, E. J., & Kostadinova, T. (2005). Assessing the effectiveness of international environmental agreements: The case of the 1985 Helsinki protocol. *American Journal of Political Science*, 49, 86–102. <https://doi.org/10.2307/3647715>
- Rodrigues, L., Bach, L., Biraschi, L., Dubourg-Savage, M.-J., Goodwin, J., Harbusch, C., Hutson, T., Ivanova, T., Lutsar, L., & Parsons, K. (2006). Wind Turbines and Bats: Guidelines for the planning process and impact assessments (Version 1.0, September 2006). Annex1 to Resolution 5.6 of the 5th Session of the Meeting of Parties. Ljubljana, Slovenia. https://www.eurobats.org/sites/default/files/documents/pdf/Meeting_of_Parties/MoP5_Record_Annex9_Res5_6_wind_turbines_incl_tables.pdf. <https://doi.org/10.1109/IEMBS.2006.259221>
- Rodrigues, L., Bach, L., Dubourg-Savage, M., Karapandza, B., Kovac, D., Kervyn, T., Dekker, J., Kepel, A., Bach, P., Collins, J., Harbusch, C., Park, K., Micevski, B., & Minderman, J. (2015). *Guidelines for consideration of bats in wind farm projects - revision 2014, EUROBATS publication series no. 6 (English version)*. Bonn.
- Roemer, C., Bas, Y., Disca, T., & Coulon, A. (2019). Influence of landscape and time of year on bat-wind turbines collision risks. *Landscape Ecology*, 34, 2869–2881. <https://doi.org/10.1007/s10980-019-00927-3>
- Roscioni, F., Russo, D., Di Febbraro, M., Frate, L., Carranza, M. L., & Loy, A. (2013). Regional-scale modelling of the cumulative impact of wind farms on bats. *Biodiversity and Conservation*, 22, 1821–1835. <https://doi.org/10.1007/s10531-013-0515-3>
- Rydell, J., Bach, L., Dubourg-Savage, M.-J., Green, M., Rodrigues, L., & Hedenström, A. (2010). Bat mortality at wind turbines in northwestern Europe. *Acta Chiropterologica*, 12(2), 261–274. <https://doi.org/10.3161/150811010X537846>
- Santos, H., Rodrigues, L., Jones, G., & Rebelo, H. (2013). Using species distribution modelling to predict bat fatality risk at wind farms. *Biological Conservation*, 157, 178–186. <https://doi.org/10.1016/j.biocon.2012.06.017>
- Staid, A., & Guikema, S. D. (2013). Statistical analysis of installed wind capacity in the United States. *Energy Policy*, 60, 378–385. <https://doi.org/10.1016/j.enpol.2013.05.076>
- Verboom, B., & Huitema, H. (1997). The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. *Landscape Ecology*, 12, 117–125. <https://doi.org/10.1007/BF02698211>
- Voigt, C. C., Lindecke, O., Schönborn, S., Kramer-Schadt, S., & Lehmann, D. (2016). Habitat use of migratory bats killed during autumn at wind turbines. *Ecological Applications*, 26, 771–783. <https://doi.org/10.1890/15-0671>
- Whitby, M. D., Schirmacher, M. R., & Frick, W. F. (2021). *The state of the science on operational minimization to reduce bat fatality at wind energy facilities. A report submitted to the National Renewable Energy Laboratory*. Bat Conservation International.
- Wieringa, J. G., Carstens, B. C., & Gibbs, H. L. (2021). Predicting migration routes for three species of migratory bats using species distribution models. *PeerJ*, 9, e11177. <https://doi.org/10.7717/peerj.11177>

SUPPORTING INFORMATION

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

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Supporting Information – Over a decade of failure to implement UNEP/EUROBATS guidelines in wind energy planning: a call for action

Supporting Methods

1) Assessing the cumulated number of wind turbines in relation with the distance to the nearest woody edge

Accurate, high-resolution land-cover and hedgerow data were only available for France, we therefore adopted different methodological approaches between countries to assess the cumulated number of wind turbines in relation with the distance to the nearest woody edge. Furthermore, as the computation of distances between wind turbines and woody edges was done manually for German and British data and automatically for French data, we could only consider the period 2009-2020 (i.e. period starting one year following the publication of the UNEP/EUROBATS guidelines) for the formers whereas we could focus on the whole period (1991-2020) for the latter.

France

We extracted data on operational wind turbines spanning the years 1991 to 2020 from regional environmental planning authorities (Table S1). Date of construction was available for 4,658 out of 8,066 wind turbines. We used the French high-resolution land-cover data (CES OSO, <http://osr-cesbio.ups-tlse.fr/oso/>, 10 m resolution) and data from the French National Bocage Monitoring System (IGN, BD Haie, <https://geoservices.ign.fr/>) to map forest cover and hedgerows at the national scale, respectively. We then automatically computed the Euclidean distance between each wind turbine and the nearest forest patch or hedgerow using a custom function (https://github.com/LMariton/Extract_distances) in R v.4.1.0 (R Development Core Team, 2021). Then, we assessed the cumulated number of wind turbines in relation with the distance to the nearest woody edge for the whole period (1991-2020) and for the periods before (1991-2008) and after (2009-2020) the initial UNEP/EUROBATS guidelines publication in 2008. This was done at both national and regional scales. It should be noted that computing

periods before and after 2008 were performed considering only regions for which sufficient information on the year of wind turbine construction was available (i.e. Bourgogne-Franche-Comté, Bretagne, Centre-Val de Loire, Hauts-de-France, Occitanie, and Pays de la Loire). Data on construction year for the Hauts-de-France region were provided by the environmental authority but are not publicly available.

Germany and the UK

In the UK and Germany, the lack of national-scale high-resolution land-cover or hedgerow data meant we had to manually measure distances between wind turbines and woody edges. Since manually measure the distance between each wind turbine in Germany and the UK and the nearest woody edge was not feasible, we were forced to proceed to a sampling of wind turbines. We randomly selected roughly 1,000 wind turbines constructed after 2009 per country, and manually computed distances from nearest woody edges using satellite imagery (when possible), leading to 1,002 and 818 wind turbines selected in Germany and the UK, respectively. We then assessed the cumulated number of wind turbines in relation with the distance to the nearest woody edge.

Wind turbines in Germany were accessed from each federal state of Germany, either from publicly available online platforms or not publicly available data provided by the federal authority for this research project, respectively (Table S1). Locations of wind turbines in the UK were not publicly available. Instead, we used the publicly available locations of operational wind farms (Table S1). Since the data collected did not have the same resolution (x,y coordinates of each single wind turbine for Germany and x,y coordinates of centroid of each wind farm for the UK), we applied different methods to select a subset of wind turbines. For Germany, we randomly selected roughly 1,000 wind turbines. For each wind farm in the UK, we systematically selected (whenever possible) two wind turbines: one located at the centre of the farm, and one located at its most western point. This resulted in a selection of 1,104 wind turbines.

Using QGIS v.3.18.3 (2021, <http://qgis.org>) coupled with Google Satellite Imagery, we manually measured the Euclidean distance between wind mast and the nearest woody edge (either hedgerow or forest). To make our results comparable to the French case, we used the same definition of hedgerow as described in the French National Bocage Monitoring System (IGN, BD Haie, <https://geoservices.ign.fr/>). We acknowledge that small woody features such as hedgerows may have been planted between 2009 and 2020, but current states of knowledge on hedgerows in many European countries indicate a decline rather an increase of total length of woody linear features, especially in rural areas (Wright, 2016). Measurements were

conducted by five people who had been randomly allocated roughly the same number of wind turbines per country (between 200-207 wind turbines per person for Germany, and 220-224 for the UK). To limit observer bias, we calibrated our measurements during training sessions. A confidence score was attributed to each measurement (0: not confident or absence of wind turbine in the satellite image, 1: confident). We subsequently restricted our data to measurements taken with confidence, leading to 1,002 (two additional wind turbines were accidentally measured by one of the observers) out of 1,000 and 818 out of 1,104 wind turbines selected in Germany and the UK, respectively.

Table S1. Download links for wind turbine location maps.

Country	Region/Land	Download link
France	Auvergne-Rhone-Alpes region	https://catalogue.data.gouv.fr/geosource/panierDownloadFrontalParametrage?LAYERIDTS=14008027
	Bourgogne-Franche-Comte region	https://www.data.gouv.fr/fr/datasets/r/57006312-2e13-4482-bfb4-fd59e91c47bd
	Bretagne region	https://geobretagne.fr/geoserver/dreal_b/wfs?SERVICE=WFS&VERSION=2.0.0&REQUEST=getfeature&typename=n_mat_eolien_p_r53&outputformat=shape-zip
	Centre-Val-de-Loire region	https://carmen.developpement-durable.gouv.fr/11/DREAL24.map&service=DownloadLayer
	Corse region	https://georchestra.ac-corse.fr/geonetwork/srv/fre/catalog.search#/metadata/MT1326817955942
	Grand-Est region	http://catalogue.geo-ide.developpement-durable.gouv.fr/catalogue/srv/fre/catalog.search?jsessionid=966E946F78AB1C55F8C57287835622D3.tc_geoide-catalogue-fo-inter_171_25#/metadata/fr-120066022-jdd-f1d59026-07e1-4b18-b4f0-6539190abf3d
	Hauts-de-France region	http://catalogue.geo-ide.developpement-durable.gouv.fr/catalogue/srv/fre/catalog.search?jsessionid=966E946F78AB1C55F8C57287835622D3.tc_geoide-catalogue-fo-inter_171_25#/metadata/fr-120066022-jdd-f20f8125-877e-46dc-8cf8-2a8a372045eb
	Ile-de-France region	http://catalogue.geo-ide.developpement-durable.gouv.fr/catalogue/srv/fre/catalog.search?jsessionid=966E946F78AB1C55F8C57287835622D3.tc_geoide-catalogue-fo-inter_171_25#/metadata/fr-120066022-jdd-787d6616-8bb4-4baf-8eb9-9ada6d7a44f7
	Normandie region	http://catalogue.geo-ide.developpement-durable.gouv.fr/catalogue/srv/fre/catalog.search?jsessionid=966E946F78AB1C55F8C57287835622D3.tc_geoide-catalogue-fo-inter_171_25#/metadata/fr-120066022-jdd-2db8244f-81be-4edc-a229-c843fef27c69
	Nouvelle-Aquitaine region	https://catalogue.sigena.fr/geosource/panierDownloadFrontalParametrage?LAYERIDTS=4289499
	Occitanie region	https://data.laregion.fr/explore/dataset/dreal-occitanie-mats-eoliens-en-occitanie/export/
	Provence-Alpes-Côte d'Azur region	https://geo.data.gouv.fr/fr/datasets/7ae6cf99ba6e661811da1c592d7f73f6a3e038b8
Germany	Pays-de-la-Loire region	https://data.paysdelaloire.fr/explore/dataset/234400034_eolien-terrestre-mats-deoliennes-en-pays-de-la-loire0/export/
	Bavaria	https://www.energieatlas.bayern.de/karten/?lang=de&topic=energie_gesamt&bgLayer=atkis
	Baden-Wuerttemberg	https://udo.lubw.baden-wuerttemberg.de/public/pages/map/default/index.xhtml?mapId=2ab5fab4-0d14-4aa5-a90c-4870b7369ce0&overviewMapCollapsed=false&mapSrs=EPSG%3A25832&mapExtent=231102.23592430277%2C5249216.819657371%2C777026.6980756973%2C5534121.148342631
	Brandenburg	https://geoportal.brandenburg.de/detailansichtdienst/render?view=gdiib&url=https://geoportal.brandenburg.de/gs-json/xml?fileid=45C506E5-3E9D-4DE2-9073-C3DB636CE7CF
	Hesse	https://www.hlnug.de/themen/luft/windenergie-in-hessen
	Mecklenburg-Western Pomerania	https://www.geoportal-mv.de/portal/Geowebdienste/Fachthemen/Energie
	Lower Saxony	https://energieatlas.niedersachsen.de/startseite/datenabgabe/datenabgabe-energieatlas-niedersachsen-163630.html
	North Rhine-Westphalia	https://open.nrw/dataset/2dd18cf8-edc7-4e7f-8424-c4c72feb437f
	Rhineland-Palatinate	http://map1.sgd.nord.rlp.de/kartendienste_rok/index.php?service=energieportal
	Saarland	https://geoportal.saarland.de/mapbender/frames/index.php?mb_user_myGui=Geoportal-SL-2020&LAYER[zoom]=1&LAYER[visible]=1&LAYER[querylayer]=1&LAYER[id]=36902
	Saxony	https://www.luft.sachsen.de/windkraftanlagen-15643.html
	Saxony-Anhalt	https://lau.sachsen-anhalt.de/naturschutz/datenabgabe/
UK	Schleswig-Holstein	https://opendata.schleswig-holstein.de/dataset/windkraftanlagen
	Thuringia	https://www.geoportal-th.de/de-de/Metadaten/Metadatenansicht/uid/1e33eaa7-aeff-43cc-8374-e076099c6bff/sid/0
	<i>all regions</i>	https://www.gov.uk/government/publications/renewable-energy-planning-database-monthly-extract

2) Assessing changes in wind turbines siting over time in France

To assess whether changes in wind turbines siting occurred in France after the publication of the European guidelines in 2008, we performed generalized linear mixed-effects models (GLMMs, “glmmTMB” R-package; Brooks *et al.*, 2017) with a negative binomial distribution to handle right-skewed and long-tailed distribution and overdispersion. Wind turbine distance from woody edges was included as a response variable while year of wind turbine construction and its quadratic term were considered as fixed effects. The latter was added to detect possible non-linear relationship. We conducted GLMMs at both national and regional scales, considering only regions for which sufficient information on the year of wind turbine construction was available (i.e. Bourgogne-Franche-Comté, Bretagne, Centre-Val de Loire, Hauts-de-France, Occitanie, and Pays de la Loire). It should be noted that construction years for the Hauts-de-France region were provided by the environmental authority but are not publicly available. To account for within- region and wind farm dependency in the measurements, we included wind farm ID nested within region ID as random effects into the model performed at the national scale. Wind farm ID was included as random effect for models at the regional scale. Given that residuals of most models were spatially autocorrelated (Moran’s I test, $p\text{-value} < 0.05$), we also added a spatial autocovariate as a fixed effect in these models. The spatial autocovariate is a distance-weighted function of neighbouring response values to the model’s explanatory variables and was computed using the `autocov_dist` function (“spdep” R-package; Bivand, 2020). When including this variable, Moran’s I test was no longer significant ($p\text{-value} > 0.05$).

Thus, full models were written as follows:

(i) National scale:

Distance between wind turbine and woody edges ~ Year of wind turbine construction + (Year of wind turbine construction)² + autocov_dist (when required) + 1|Region ID/wind farm ID

(ii) Regional scale:

Distance between wind turbine and woody edges ~ Year of wind turbine construction + (Year of wind turbine construction)² + autocov_dist (when required) + 1| wind farm ID

Overall model validation was then performed using diagnostic plots with the “DHARMA” (Hartig, 2021) and “performance” (Lüdecke *et al.*, 2021) R-packages. Full models were compared to null ones using the Akaike information criterion (Burnham and Anderson, 2002),

and goodness-of-fit was assessed using the marginal R^2 (variance explained by the fixed effects) and conditional R^2 (variance explained by both fixed and random factors) values (Nakagawa and Schielzeth, 2013). Results are displayed in Table S2 and 2. All the analyses were conducted in R v.4.1.0 (R Development Core Team, 2021).

Supporting Results

Table S2. Comparison of full and null models built to assess changes in wind turbines siting distances from woody edges in France over time at both national and regional scales.

Scale	Model	K	AIC	ΔAIC	mR^2	cR^2
France N = 4,658	Full model	6	56137.3	0.00	<0.01	0.91
	Null model	3	56140.9	3.60	-	-
Bourgogne-Franche-Comté N = 345	Full model	6	3892.33	0.00	0.20	0.62
	Null model	3	3913.65	21.32	-	-
Bretagne N = 609	Full model	5	5948.84	0.00	0.01	0.23
	Null model	3	5948.41	-0.43	-	-
Centre-Val de Loire N = 503	Full model	6	6850.05	0.00	0.24	0.47
	Null model	3	6916.26	66.21	-	-
Hauts-de-France N = 1,764	Full model	6	23706.9	0.00	0.01	0.01
	Null model	3	23715.6	8.70	-	-
Occitanie N = 815	Full model	6	8350.67	0.00	0.20	0.78
	Null model	3	8402.90	52.23	-	-
Pays de la Loire N = 514	Full model	5	5708.58	0.00	0.02	0.5
	Null model	3	5601.61	-106.97	-	-

N: number of wind turbines

K: number of parameters AIC: Akaike information criterion

ΔAIC : difference in AIC between the null model and the full model

mR^2 : marginal R-squared

cR^2 : conditional R-squared

Table S3. Summary per year of the total number of operating wind turbines (WT), the total number of operating WT at less than 200 m from woody edges and the total number of operating WT at more than 200 m from woody edges, in France for which our analyses were based on an exhaustive dataset.

Year	Number of WT of WT	Number of WT installed at less than 200 m from woody edges	Number of WT installed at more than 200 m from woody edges
1991	1	0	1
1993	4	0	4
1999	5	5	0
2000	30	20	10
2001	31	15	16
2002	55	23	32
2003	89	77	12
2004	37	36	1
2005	80	60	20
2006	294	195	99
2007	151	111	40
2008	250	160	90
2009	228	177	51
2010	189	148	41
2011	116	65	51
2012	106	81	25
2013	126	97	29
2014	129	82	47
2015	88	70	18
2016	293	229	64
2017	181	139	42
2018	203	155	48
2019	135	109	26
2020	73	63	10
Total	2894	2117	777

References

- Bivand, R., 2020. spdep: Spatial Dependence: Weighting Schemes, Statistics. R package version 1.1-5. Available at <https://cran.r-project.org/web/packages/spdep/index.html>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, 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.
- Burnham, K.P., Anderson, D.R., 2002. A practical information-theoretic approach. *Model selection and multimodel inference* 2.
- Hartig, F., 2021. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.3. Available at <https://cran.r-project.org/web/packages/DHARMA/index.html>.
- Lüdtke, D., Makowski, D., Ben-Shachar, M., Patil, I., Waggoner, P., Wiernik, B., 2021. Performance: assessment of regression models performance. R package version 0.7.3. Available at <https://cran.r-project.org/web/packages/performance/index.html>.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in ecology and evolution* 4, 133-142.
- R Development Core Team, 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Wright, J., 2016. A natural history of the hedgerow and ditches, dykes and stone walls. Profile Books, London, UK.

Prise en compte des effets de la pollution lumineuse sur la biodiversité dans les mesures de conservation : défis et perspectives

Résumé :

Ce dernier siècle, les lumières électriques ont proliféré, modifiant l'environnement nocturne. Des études scientifiques alertent sur les effets négatifs de la lumière artificielle nocturne (LAN) qui perturbe de nombreux processus écologiques et taxons. Notre objectif a ainsi été de combler des manques de connaissances afin d'aider à une meilleure considération des effets de la pollution lumineuse sur la biodiversité dans les mesures de conservation. Nous avons utilisé les chiroptères comme modèles biologiques car ce sont de bons bioindicateurs de l'effet des pressions anthropiques sur la biodiversité et, étant nocturnes, ils sont directement exposés à la LAN.

Nous avons préconisé de considérer la distribution temporelle des espèces dans les mesures de conservation, un prérequis étant de connaître leur écologie temporelle. Nous avons utilisé les données d'un programme national de suivis acoustiques des chiroptères (Vigie-Chiro) pour étudier leur rythme d'activité nocturne (9807 nuits, 20 espèces). Nous avons montré que les espèces pouvaient être séparées en trois groupes ayant une activité crépusculaire, en cœur de nuit ou intermédiaire, avec des variations des rythmes d'activité selon les saisons. La prise en compte de ces rythmes complexes aiderait à concevoir des mesures de conservation efficaces, par exemple, en définissant des extinctions partielles de la LAN adaptées à des espèces cibles.

La plupart des chiroptères émergeant tôt sont des espèces « tolérantes à la lumière » pouvant se nourrir sous les lampadaires. Cependant, à l'échelle du paysage, ces espèces semblent moins abondantes à cause de la LAN. Cela pourrait s'expliquer par des perturbations de leur rythme d'activité influant possiblement les dynamiques de population. A l'aide des données Vigie-Chiro, nous avons testé si la LAN induisait de telles perturbations pour une de ces espèces (*Eptesicus serotinus*). La LAN, et dans une moindre mesure la lumière de la lune, réduisaient son abondance. La LAN retardait son activité, ce décalage était amplifié par la couverture nuageuse, possiblement à cause de son effet amplificateur du halo lumineux. Des analyses complémentaires ont suggéré que la LAN retardait l'activité de deux autres espèces « tolérantes à la lumière ». Ainsi, même ces espèces devraient être protégées de la LAN.

Lorsqu'éclairer est nécessaire, changer l'intensité, la direction ou le spectre des éclairages sont des mesures de réduction possibles. Nous assistons à une modernisation des éclairages avec des diodes électroluminescentes (LEDs). Malgré des impacts potentiels sur la biodiversité, peu d'études se sont intéressées à cette évolution. En réanalysant les données d'une étude publiée, nous avons montré que les changements de spectre et d'intensité accompagnant cette évolution avaient des effets additifs et interactifs sur les chiroptères. Quand l'intensité des LEDs augmentait, leur activité décroissait. Avec les données Vigie-Chiro, nous avons montré que les LEDs pouvait réduire la connectivité du paysage pour les chiroptères, cet impact étant atténué en orientant mieux les lumières. Nous avons recommandé d'utiliser des LEDs avec des couleurs plus chaudes et de moindre intensité.

Evaluer l'effet de la LAN sur la biodiversité implique des approches spatio-temporelles multi-échelles. Malgré les manques, il y a désormais suffisamment de preuves de l'impact de la LAN sur les écosystèmes. Les mesures de réduction étant en développement, évaluer leur efficacité et les améliorations possibles est indispensable. Penser la réduction de la LAN à l'échelle du paysage est une évolution impérative, d'où l'émergence du concept de trame noire. Un projet transdisciplinaire sur les pratiques communales d'éclairage et leurs évolutions a été initié pendant cette thèse. En effet, puisque la LAN n'a pas que des implications écologiques, mais aussi sanitaires et socio-culturelles, une perspective transdisciplinaire est indispensable pour changer nos façons d'éclairer.

Mots clés : Pollution lumineuse, Chiroptères, Mesures de conservation, Suivis acoustiques passifs, Rythmes d'activité

Taking light pollution effects on biodiversity into account in conservation measures: challenges and prospects

Abstract:

Electric lights have proliferated rapidly over the last century and have changed the night-time environment globally. Over the past decades, scientific studies have shown the effects of artificial light at night (ALAN) on biodiversity. Light pollution has been shown to disrupt a wide range of ecological processes and taxa. In this PhD, we aimed to fill some of the knowledge gaps that could prevent the effects of light pollution on biodiversity from being effectively addressed by mitigation measures. We used bats as model species because they are considered good indicators of the effect of anthropogenic pressures on biodiversity and because, being nocturnal, they are directly exposed to ALAN.

We advocated considering the temporal distribution of species in conservation measures, a prerequisite being to have access to knowledge on their temporal ecology. We used data from a national bat monitoring program (Vigie-Chiro) based on acoustic monitoring to characterise bat diel activity patterns (9807 nights monitored, 20 species). We found that bat species could be separated into three functional groups characterised by a crepuscular activity, an activity that occurs when it is completely dark or an intermediate activity. We showed variations of diel activity patterns depending on the season. Accounting for these complex diel activity patterns would help to design efficient mitigation measures. For instance, it would allow the design of part-night lighting schemes covering the range of activity of the target species.

Early emerging bats are mostly “light tolerant” species known to feed on insects attracted to lights. However, at the landscape scale, these species tend to be less abundant because of ALAN. This could be explained by disruptions in the diel activity patterns of bats due to ALAN, with potential consequences for population dynamics. Using the Vigie-Chiro dataset, we tested whether ALAN was responsible for such disruptions on a “light tolerant” species (*Eptesicus serotinus*). ALAN, and to a lesser extent moonlight, reduced its abundance. ALAN delayed activity, this delay was amplified during overcast nights, probably because cloud cover amplified skyglow. Further analyses suggested that two other “light tolerant” species might delay their activity because of ALAN. Thus, even “light tolerant” species should be protected from light pollution.

Where it is not possible to switch off lights, other mitigation measures include changing the intensity, directionality and spectrum of light. Many countries are retrofitting lighting equipment with light emitting diodes (LEDs). Despite potential impacts on biodiversity, few studies have focused on this shift. By reanalysing the data from a previously published study, we found that changes in light spectrum and intensity during such a shift have additive and interactive effects on bats. Bat activity decreased with increasing LED intensity. Using the Vigie-Chiro dataset, we showed that the adoption of LEDs would decrease landscape connectivity for bats, with this impact possibly being mitigated by better orienting the light flux. We recommended using LEDs with warmer colours and reduced light intensity.

Multiscale spatiotemporal approaches are needed to assess ALAN effect on biodiversity. Although some knowledge gaps remain, there is overwhelming evidence of the impact of light pollution on ecosystems. Mitigation measures are being developed, so there is a need to assess their effectiveness and possible improvements. Considering the reduction of ALAN at the landscape scale is a necessary next step, hence the emergence of the concept of dark ecological networks. A transdisciplinary project on lighting practices and their evolution in municipalities was initiated during this PhD. Indeed, as ALAN has not only ecological but also health and socio-cultural implications, a transdisciplinary perspective is needed to shift the paradigm from conventional lighting to new forms of lighting.

Keywords: Light pollution, Bats, Passive acoustic monitoring, Diel activity patterns, Conservation measures