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Impacts of light pollution on bat spatiotemporal dynamics in France: implications for outdoor lighting planning

Clémentine Azam

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THESE

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Présentée publiquement par

Clémentine Azam

Le 12 Décembre 2016

**Impacts of light pollution on bat spatiotemporal
dynamics in France**

Implications for sustainable outdoor lighting planning

Sous la direction de : **Dr. Isabelle Le Viol, Dr. Christian Kerbiriou, Pr. Denis
Couvét (HDR)**

JURY :

M. Arlettaz, Raphaël	Professeur, Université de Berne (Suisse)	Rapporteur
M. Barbaro, Luc	Chargé de recherches, INRA Toulouse	Rapporteur
Mme. Lecomte, Jane	Professeure, Université Paris-Sud	Examinatrice
Mme. Frascaria-Lacoste Nathalie	Professeure, AgroParisTech, Université Paris-Sud	Examinatrice
M. Newson, Stuart	Senior Research Ecologist, British Trust for Ornithology	Examineur
M. Kerbiriou, Christian	Maitre de Conférences, Université Pierre et Marie Curie	Directeur de Thèse
Mme. Le Viol, Isabelle	Maitre de Conférences, Muséum National d'Histoire Naturelle	Directrice de Thèse

FOREWORD

What if we woke up one morning only to realize that all of the conservation planning of the last thirty years only told half of the story- the daytime story?

Catherine Rich & Travis Longcore, 2006

Until the last decade or so, the impacts of public outdoor lighting on biodiversity received little or no attention from policymakers, stakeholders but also scientists. Outdoor lighting has only been perceived as a way to ensure the security and safety of people, and more recently as a way to save energy. However, the ongoing technological revolution in lighting design, characterized by the emergence of Light Emitting Diodes and adaptive lighting innovations (digital tools, Apps, etc.), has impulsed awareness about the need to broaden outdoor lighting policies beyond security issues in order to take in to account the influence of artificial lighting on social interactions, human well-being, and biodiversity. It actually appears that outdoor lighting management is becoming a key aspect of the concept of “smart cities”, and hence involves a whole range of disciplines such as physics, sociology, politics, economics and finally biology (including ecology).

In this general context, as a conservation biologist, I intended during this PhD not only to characterize the impacts of nighttime artificial lighting on nocturnal organisms, but also to propose practical outdoor lighting recommendations that can limit the adverse impacts of lighting on biodiversity. Hence, in parallel to my personal research, I got involved in the

“Loss Of the Night Network” (EU-COST; <http://www.cost-lonne.eu/>), which is a research network that aims at promoting an interdisciplinary view of outdoor lighting and at elaborating integrated and consistent outdoor lighting recommendations that effectively limit light pollution issues. I am also currently contributing to the IPBES regional assessment on biodiversity and ecosystem services for Europe and Central Asia (Intergovernmental Platform on Biodiversity and Ecosystem Services; Deliverable 2b; Chapter 4) for a sub-chapter on the impacts of light pollution on biodiversity. Additionally, during my PhD, I got the chance to work with different local stakeholders such as conservationists and mayors in the Natural Park where I did my fieldwork, and light designers during the Light Design training school I attended in 2015 (LiDe3 Training School, TU-Berlin, November 2015). Hence, these exchanges and collaborative projects have allowed me to emphasize the opportunities and constraints other disciplines may face regarding outdoor lighting regulations. Hence, I decided to organize this PhD at the interface between science and policies in order to investigate how my results from ecological research can be integrated in outdoor lighting regulations.

Abstract

Light pollution induced by the widespread use of nighttime artificial lighting is a global change affecting substantial part of terrestrial and marine ecosystems. As a result, major concerns have been raised about its hidden impacts on biodiversity and ecosystem functioning. Light pollution has major impacts on the circadian and seasonal cycles of organisms, and on their movements and spatial distributions. As a whole, light pollution likely disrupts the spatiotemporal dynamics of biological communities and ecosystems.

In this context, the aim of this PhD was to characterize the impacts of nighttime artificial lighting on bat activity (order: chiroptera) at multiple spatial scales in order to propose reduction measures that can effectively limit the adverse impacts of light pollution on biodiversity. We used bats as model species as they are nocturnal and directly exposed to light pollution and they are considered to be good indicators of the response of biodiversity to anthropogenic pressure.

We first intended to characterize the extent of effect of light pollution at a landscape scale relative to major land-use pressures that are threatening biodiversity worldwide. Using a French national-scale citizen science database, we found that landscape-scale level of light pollution negatively affected common bat species, and that this effect was significantly stronger than the effect of impervious surfaces but weaker than the effect of intensive agriculture. This highlighted the crucial need to account for outdoor lighting in land-use planning in order to restore darkness in human-inhabited landscapes.

Thus, through an *in situ* experiment, we investigated whether i) restoring darkness in a landscape for a part of the night through part-night lighting schemes, or ii) restraining the spatial extent of lighting at the vicinity of natural elements were effective options to enhance dark ecological corridors in human-inhabited landscapes. We found that part-night lighting schemes were unlikely to effectively mitigate the impacts of artificial lighting on light-sensitive species. However, we revealed that streetlights should be separated from ecological corridors by at least 50 m, and that the light trespass should be lower than 0.1 lux to allow their effective use by light-sensitive species.

Overall, this PhD thesis revealed the major importance of addressing light pollution issues at multiple spatial scales to characterize its impacts on biodiversity. It also exposed the crucial importance of integrating outdoor lighting in land-use planning strategies and proposed to implement ecological criteria in future European standards for outdoor lighting.

Résumé

La pollution lumineuse, induite par l'utilisation massive d'éclairage artificiel la nuit, est un changement global qui affecte une partie importante des écosystèmes terrestres et marins, et qui soulève de nombreuses inquiétudes quant à son influence sur la biodiversité et le fonctionnement des écosystèmes. En effet, la pollution lumineuse induit de nombreux impacts sur les rythmes circadiens et saisonniers des organismes, et affecte leurs mouvements et leurs distributions spatiales. L'accumulation de ces impacts dans le temps et dans l'espace sur les différentes espèces peut ainsi entraîner des perturbations en cascade sur les dynamiques spatiotemporelles des communautés et sur les écosystèmes.

Dans ce contexte, l'objectif de cette thèse est de caractériser les impacts de l'éclairage artificiel sur les activités de chauves-souris (ordre: chiroptère) à de multiples échelles spatiales afin d'élaborer des mesures de gestion de l'éclairage public qui limitent ses impacts négatifs sur la biodiversité. Nous avons utilisé les chauves-souris comme modèle d'étude car elles sont nocturnes et directement exposées à la pollution lumineuse, et sont considérées comme des espèces bioindicatrices de la réponse des espèces aux pressions anthropiques.

Dans un premier temps, nous avons caractérisé l'impact relatif de la pollution lumineuse à l'échelle du paysage par rapport aux autres pressions de changements d'usage des sols en utilisant une base de données nationale de sciences participatives. Nous avons trouvé que la pollution lumineuse avait un impact négatif sur l'activité et la probabilité de présence des espèces de chiroptères les plus communes en France, et que cet impact était significativement plus fort que celui de l'artificialisation des sols, mais moins important que celui de l'agriculture intensive. Ces résultats confirment l'importance de prendre en compte l'éclairage public dans les stratégies d'aménagement du territoire pour restaurer efficacement de l'obscurité dans les paysages anthropisés.

Ainsi, nous avons élaboré une expérience *in situ* pour déterminer si i) restaurer de l'obscurité dans le temps en éteignant les lampadaires pour une partie de la nuit (extinction nocturne), ou ii) limiter l'étendue spatiale de l'éclairage à proximité d'éléments naturels pouvaient être des mesures efficaces pour créer des zones corridors et des zones de refuges obscurs dans les paysages anthropisés. Nos résultats ont montré que les mesures actuelles d'extinction ne limitaient pas efficacement l'impact de l'éclairage sur les espèces de chiroptères sensibles à la lumière. Par contre, nous avons déterminé que les lampadaires devraient être séparés d'au moins 50 m des corridors écologiques, et que l'intrusion de lumière dans la

végétation autour des zones éclairées ne devrait pas dépasser 0.1 lux pour permettre l'utilisation de ces espaces par les espèces sensibles à la lumière.

En conclusion, cette thèse a mis en lumière l'importance de traiter la question de la pollution lumineuse à de multiples échelles spatiales pour bien caractériser ses impacts sur la biodiversité. Elle a par ailleurs permis de souligner l'importance de la prise en compte de cette pollution dans l'aménagement du territoire, et de proposer des critères écologiques qui pourraient être intégrés dans les futur normes et standards européens pour l'éclairage public.

Remerciements

En premier lieu, je tiens à remercier les membres de mon jury, **Pr. Raphaël Arlettaz**, **Dr. Luc Barbaro**, **Pr. Jane Lecomte**, **Pr. Nathalie Frascaria-Lacoste** et **Dr. Stuart Newson**, d'avoir accepté d'évaluer mes travaux de thèse.

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GENERAL INTRODUCTION

1. Light pollution in a changing world

Land-use change, induced by socio-economical shifts in human activities, has become since the industrial revolution a major driver of global biodiversity loss and of ecosystem functions alterations (Venter et al. 2016; Newbold et al. 2016). These changes are characterized by a dramatic intensification of agriculture following worldwide human population exponential growth, and by a major increase in urban migration (Figure 1; Foley et al. 2005). In particular, over half of the world's population currently lives in urban areas, and this proportion is expected to reach 66 % by 2050 (UN 2014). This shift in human way of life has led to a dramatic increase in the size of urban areas and a major development of transport infrastructures for the commuting of goods, resources and people (Figure 1; Foley et al. 2005; Grimm et al. 2008a). At a local scale, urbanization process is characterized by extreme forms of habitat loss and fragmentation with only small and isolated patches of vegetation remaining in an impervious matrix (Savard et al. 2000). At a regional scale, it generates growing pressures on peripheral ecosystems by subjecting them to major changes in soil and habitat composition through residential, commercial and industrial development (Grimm et al. 2008a, 2008b). This urban sprawl mostly concerns rural and semi-natural landscapes, but also threatens protected areas which distance to the nearest urban area is decreasing over time (McDonald et al. 2009). Overall, urbanization process dramatically alters environmental biotic and abiotic conditions by generating habitat loss and fragmentation at multiple spatial scales (Foley et al. 2005; Grimm et al. 2008b). As a result, it induces some shifts in biological communities by decreasing the abundance of specialist species for the benefits of generalists (Devictor et al. 2007; Penone et al. 2013; Deguines et al. 2016),

which in turn engenders biotic homogenization (McKinney 2006) and loss of ecosystem services such as pollination (Deguines et al. 2014). In this context, limiting the adverse impacts of urbanization on biodiversity has become a major issue in conservation biology and land-use planning (Savard et al. 2000).

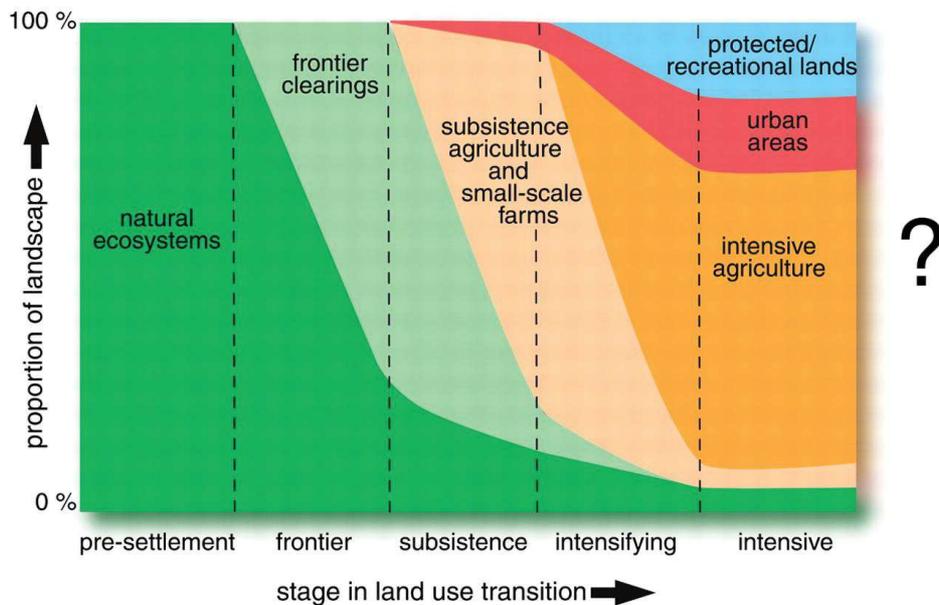


Figure 1. Extracted from Foley et al. (2005) showing expected land-use transitions that may be experienced in a given region following the demographic and economic shifts of modern societies: from presettlement natural vegetation to frontier clearing, then to subsistence agriculture and small-scale farms, and finally to intensive agriculture, urban areas, and protected recreational lands (e.g. Western Europe).

However, urbanization process does not only impact biodiversity through the loss and fragmentation of natural habitat induced by the increase of impervious surface. It is also associated with the emission of environmental stressors such as chemical, noise and light pollutions whose extent of effect on biodiversity has not always been assessed, although it may be essential to elaborate effective land-use planning strategies (Grimm et al. 2008b). In particular, light pollution is generated by the use of artificial light at night around human infrastructures such as cities, monuments, industrial and commercial plants, and transport infrastructures (Hale et al. 2013). Although light pollution is intrinsically associated with urban and industrial areas, it

can diffuse way beyond urban and suburban landscapes and can affect substantial parts of surrounding ecosystems (Kyba & Hölker 2013). Urban areas (in terms of impervious surfaces) has been estimated to cover approximately 3 % of global land surface (Grimm et al. 2008a; Faeth et al. 2012), whereas light pollution affects 23% of it (88% of Europe; Figure 2; Falchi et al. 2016). Furthermore, it spreads at an annual rate of 6 % worldwide (range: 0 - 20 %; Hölker et al. 2010), with temperate and Mediterranean ecosystems experiencing the greatest increase in exposure because of their high level of human densities and of economic development (Bennie et al. 2015b). Over 42 % of protected areas and most mammalian species ranges among continents have experienced significant increases in exposure to light pollution since the beginning of the 1990s (Duffy et al. 2015; Gaston et al. 2015). In this context, light pollution can be considered as an expanding global change and this raises major concerns about its hidden impacts on biodiversity and ecosystem functioning (Longcore & Rich 2004; Hölker et al. 2010b).

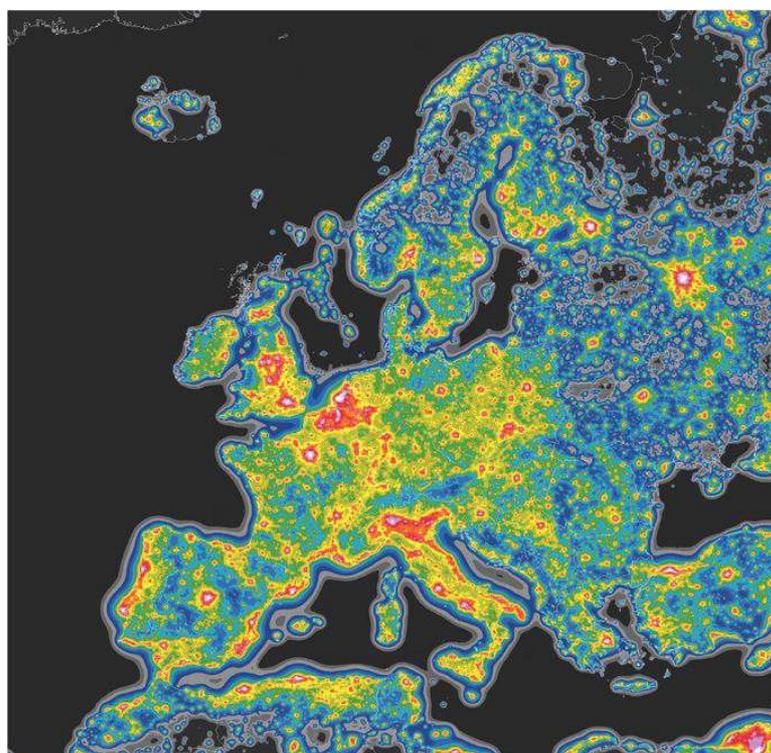


Figure 2. Map extracted from Falchi et al. (2016) presenting Europe's artificial sky brightness as a ratio to the natural sky brightness (assumed to be $174 \mu\text{cd}/\text{m}^2$).

2. The ecological impacts of light pollution on biodiversity

2.1. Context and methodology of an ongoing systematic review

During my PhD, I got involved in the COST LoNNe (“Loss of the Night Network”; <http://www.cost-lonne.eu/>) which is an interdisciplinary European network that aims at investigating the impacts of light pollution on ecosystems, human health and stellar visibility, and at elaborating recommendations for sustainable outdoor lighting planning. In this context, I have started with 3 collaborators of the network, Dr. Sibylle Schroer, Dr. Franz Hölker and Dr. Roy van Grunsven, a systematic review on the effects of artificial lighting on biodiversity, in order to propose effective lighting management recommendations for policy makers and stakeholders. This project is still under progress and is expected to be published as a policy paper at the end of 2017. The number of publications on the ecological impacts of light pollution on biodiversity has grown exponentially in the last fifteen years (Figure 3). So far, I have already extracted the literature from scientific databases (See Box 1 for details on the methodology) and classified the biological impacts of artificial lighting on bats, birds and insects which are detailed in the following section and are synthesized in the Table 1. The next step is to extract minimum threshold values for different lighting parameters to elaborate evidence-based recommendations for outdoor lighting planning (details in the General Discussion).

2.2. Alterations of species circadian and seasonal cycles

The natural alternation between day and night is an environmental cue that regulates the life cycles of both diurnal and nocturnal organisms. By inducing a large scale loss of the nighttime, artificial lighting generates major disruptions of species circadian rhythms (Navara & Nelson 2007; Robertson et al. 2010; Gaston et al. 2013; Dominoni et al. 2016). Nighttime artificial lighting inhibits melatonin secretions and alters vital biological functions such as sleep and biolo-

Box 1. Methodology for the selection of scientific articles for the systematic review

1. Paper extraction from Web Of Science

- **Data source:** peer-reviewed papers
- **Timespan:** All years.
- **Keyword search:** (ALAN) AND (TAXON [BATS or INSECTS or BIRDS])

ALAN = ("light pollution" OR "artificial light*" OR "streetlight*" OR "street light*" OR "streetlamp*" OR "street lamp*" OR "illumination" OR "illuminance" OR "outdoor lighting" OR "nighttime lighting")

BATS = ("bat" OR "chiroptera" OR "bats")

BIRDS = ("bird" OR "birds" OR "avian" OR "avifauna" OR "song" OR "singing" OR "fledging*" OR "nestling*")

INSECTS = ("insect" OR "insects" OR "arthropod*" OR "diptera" OR "moth*" OR "lepidoptera" OR "hymenoptera" OR "orthoptera" OR "cricket")

2. Paper selection

- **A "title filter:** Selection of papers that refer to artificial and natural lighting in the title, and to the taxon of interests
- **An "abstract filter":** Selection of papers that are centered on:
 - on data from fieldwork, lab experiment or monitoring (rejection of reviews and opinions)
 - on wild organisms (rejection of papers from industry such as horticulture or animal rearing)
 - on outdoor lighting (rejection of papers on indoor lighting)
- Cross-checking with Google Scholar database in order to determine if key papers are missing from the selection + Final validation by LoNNe experts.

Table 1. Number of paper extracted for birds, bats and insects after each selection steps.

Selection steps	Literature Database	Bats	Birds	Insects
Raw results	<i>Web of Science</i>	119	558	760
Title filter	<i>Web of Science</i>	36	120	107
Abstract filter	<i>Web of Science</i>	27	46	61
Add. papers from cross-checking	<i>Google scholar</i> <i>Cost LoNNe network</i>	0	12	19
Total Nb. of paper	<i>/</i>	27	58	80

-gical clock regulations (Dominoni et al. 2013c; Durrant et al. 2015; de Jong et al. 2016). Exposed passerine birds populations appear to advance their onset of daily activity (dawn chorus) from 10 to 30 minutes before sunrise, and to delay their cessation of activity 20 minutes after sunset (Nordt & Klenke 2013; Da Silva et al. 2015a; de Jong et al. 2016). Similarly, the time of emergence of female bats from maternity roosts can be significantly delayed by illuminating the monument they roost in (Downs et al. 2003; Boldogh et al. 2007). This has important implications for the reproductive success of maternities as it can decrease the growth of juveniles (Boldogh et al. 2007), and it may alter the fitness of reproductive females which can miss the peak abundance of insects at dusk (Jones & Rydell 1994).

Furthermore, nighttime artificial lighting also impacts species seasonal cycles by inducing a change in perceived day length for exposed populations. In temperate regions, this has been reported to advance the initiation of reproduction and molt in passerine birds (26 days; Dominoni et al. 2013a; Da Silva et al. 2015), and to disrupt the seasonal secretions of sexual hormones of birds and insects (Schoech et al. 2013; van Geffen et al. 2014; van Geffen et al. 2015; Russ et al. 2015). These impacts on seasonal phenology occur over large spatial scales such as in the UK where deciduous trees start budburst 7.5 days earlier in illuminated landscapes compared to dark ones (Ffrench-Constant et al. 2016). Overall, long-term exposure to nighttime artificial lighting likely alters the temporal dynamics of populations and induces important impacts on individual fitness and reproductive success (Dominoni et al. 2013; Russ et al. 2015; van Geffen et al. 2015).

2.3. *Alteration of species movements and spatial distribution*

Additionally to the impacts of light pollution on species rhythms of activity, the spatial distribution of nighttime artificial light in the landscape can also dramatically influence species movements and distributions. These impacts are of particular importance for nocturnal species because they use the nightscape to move, forage, and reproduce (Hölker et al. 2010b). The case of nocturnal insects is particularly extreme, as they present a “flight-to-light behaviour” inducing a massive attraction and trap of individuals toward light sources (Altermatt et al. 2009; van Grunsven et al. 2014). This generates an accumulation of insect biomass in illuminated patches and induces insect depletion in surrounding dark areas (Eisenbeis 2006). Insect abundance and richness are key components of ecosystems as they form the basis of most food webs (Conrad et al. 2006). Thus, the shifts in the spatial distribution of insects induced by artificial lighting likely engender cascading impacts for their predators, as it generates high quality foraging patches for light-tolerant species, while decreasing the size and quality of dark areas for light-sensitive species. As an example, the response of microchiropteran bats (insectivorous) to nighttime artificial lighting vary among species according to their foraging strategy and flight abilities (Jones & Rydell 1994). Fast-flying bat species that forage insects at dusk in the open air, such as *Pipistrellus spp.* and *Nyctalus spp.*, appear to exploit illuminated niches that present new sources of high quality and predictable foraging opportunities (Rydell 1992; Blake et al. 1994a; Lacoëuilhe et al. 2014). In contrast, slow-flying species that prey on insects in cluttered vegetation, such as *Rhinolophus spp.* and *Myotis spp.*, avoid any source of artificial lighting (Rydell 1992; Kuijper et al. 2008b; Stone et al. 2009, 2012), probably because of an intrinsic perception of increased predation risk (Jones & Rydell 1994). Hence, light pollution likely

modifies landscape use and spatial distribution of nocturnal species by inducing habitat loss for light-sensitive species, and habitat gain for light-tolerant ones.

Furthermore, nighttime artificial lighting can generate a “barrier effect” that impedes individuals’ movements through a landscape (defined as landscape connectivity). As for many other organisms, bats’ persistence in both urban and rural landscapes is highly reliant on the presence of structural connectivity elements such as tree lines, hedgerows and riverbanks that increase landscape connectivity (Hale et al. 2012; Lintott et al. 2015). In this context, the illumination of these ecological corridors by streetlights can impede the movements of both fast and slow-flying bat species (Kuijper et al. 2008a; Hale et al. 2015). As a result, these impacts on species movements may induce individual fitness costs as it may decrease the accessibility of suitable foraging areas in the landscape, and generate longer commuting distances that are associated to high energetic expenses and stress (Stone et al. 2009).

Finally, at regional or even continental scales, artificial lighting and the sky glow emitted by cities can dramatically impact the long-distance and dispersal movements of animal populations, by washing out the natural lighting signals from the moon and stars which are used by many species for navigation (Longcore & Rich 2004). The most famous example comes from the disruption of the “seafinding behavior” of nestling marine turtles emerging from underground nests which are attracted to artificial light sources along the coastline instead of the ocean (Witherington 1991; Tuxbury & Salmon 2005). This disorientation dramatically impacts nestling survival and spatial distribution of nests along beaches (Pendoley & Kamrowski 2015, 2016; Weishampel et al. 2015). This phototaxis behavior toward artificial light sources has also been reported for migrating birds (Lebbin et al. 2007; Zhao et al. 2014), and for marine bird fledglings when dispersing from colonies along coasts (Rodriguez & Rodriguez 2009; Rodríguez et al.

2015). Overall, the impacts of artificial lighting on the orientation of animals have major implications for population survival as they generate dramatic fatalities on disorientated individuals which can collide with human infrastructures such as illuminated bridges, offshore platforms and towers (Table 1; Poot et al. 2008; Longcore et al. 2013; Rodríguez et al. 2014).

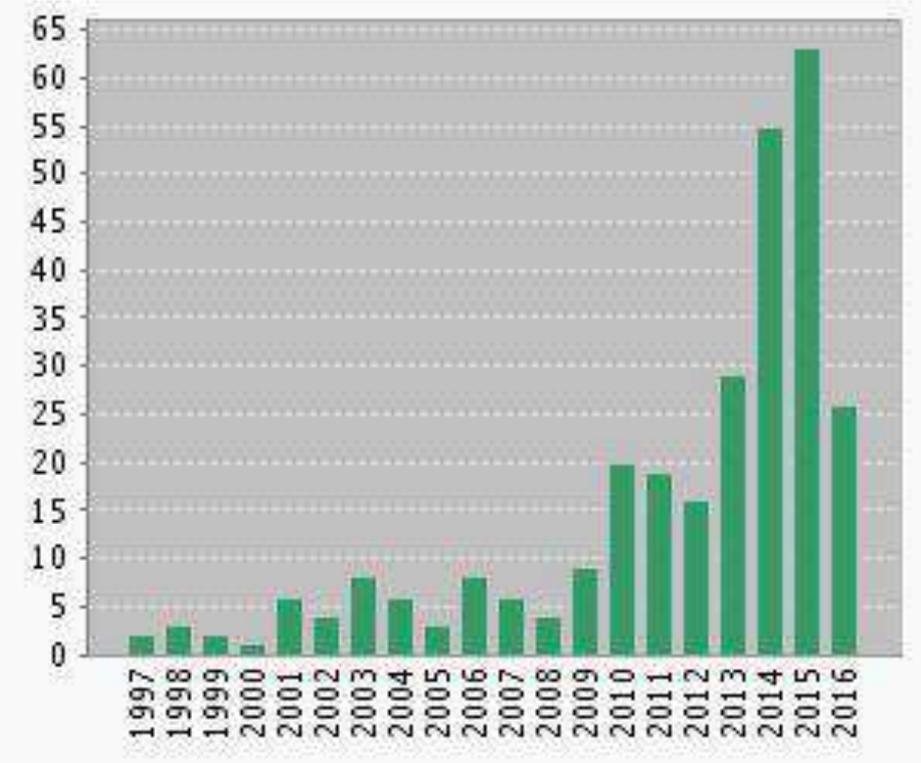


Figure 3. Number of scientific articles on the effects of nighttime artificial lighting (n = 297) on biodiversity published every year since 1997 in peer-reviewed journals (from Web of Science citation report).

Table 1. Synthesis of the known impacts of artificial lighting on birds, bats and insects. This table is part of the ongoing systematic review project I am doing in collaboration with Dr. Sibylle Schroer, Dr. Franz Hölker and Dr. Roy van Grunsven. They are in charge of the review of papers on non-flying mammals, fishes, plants, and reptiles, while I am in charge of bats, birds and insects. *n* refers to the number of papers available for each taxa.

Categories	Response	Birds (<i>n</i> =58)	Bats (<i>n</i> = 27)	Insects (<i>n</i> =80)
Circadian cycles	<i>Onset of activity</i>	Advance in activity before sunrise (10 to 30 min)	Delay in emergence from roost (up to 1h30 delay)	/
	<i>Cessation of activity</i>	Delay in activity after sunset (20 min)	/	/
	<i>Time spent foraging</i>	Increased nocturnal foraging activity	/	/
	<i>Melatonin secretion</i>	Decreased	/	Decreased
Seasonal cycles	<i>Reproduction Onset</i>	Advance in dawn chorus and in testicular growth (26 days) Disruption of female hormone secretions	/	Disruption of sex pheromone secretions Decrease in gametogenesis-gene expression
	<i>Molt</i>	Advance in molting (22 days)	/	/
Movement & Distribution	<i>Occupancy</i>	Habitat loss for marine birds colonies	Foraging habitat gain and increased quality for fast-flying species Foraging habitat loss and decreased quality for slow-flying species	Accumulation of insect biomass in illuminated areas Depletion of surrounding dark areas
	<i>Transit & Dispersal</i>	Phototaxis of dispersing fledging from marine birds colonies	Decreased landscape connectivity and gap-crossings abilities	Phototaxis toward blue and UV lights Inhibition of aquatic insects drift
	<i>Orientation & migration</i>	Phototaxis and disorientation	/	/
Population dynamics	<i>Individual fitness</i>	Lower body mass and fat score Chronic stress exposure	Increased commuting energetic costs	Decrease in immune-gene expression
	<i>Survival & mortality</i>	Increased mortality from collisions for dispersing and migrating individuals	/	Mortality and exhaustion under streetlights Decrease in predator-escape behavior
	<i>Reproductive success</i>	Long-term disruption of sexual hormone production	Decreased juvenile growth Maternity roost destruction	Decrease in egg and pupal survival Decrease in number of mated females

2.4. *Cascading impacts on biological communities*

The concomitant impacts of nighttime artificial lighting on the spatiotemporal dynamics of organisms, and the differential abilities of species to exploit illuminated niches likely induce major shifts in the balance of species interactions within biological communities. It has been suggested that the common pipistrelle *P. pipisterellus* which can forage under streetlights may be outcompeting the light-sensitive lesser horseshoe bat *R. hipposideros* which relies on the same insect resource (Arlettaz et al. 2000). Similarly, the temporal niche partitioning between diurnal and nocturnal insectivores may be blurred in illuminated areas because artificial lighting may extend the activity window of diurnal species during nighttime (Rydell & Speakman 1995; Rydell et al. 1996). Furthermore, nighttime artificial lighting may also indirectly influence organisms by interfering with interspecific trophic interactions. It has been reported that artificial lighting had a negative effect on the density of pea aphids *Acyrtosiphon pisum* in a grassland mesocosm by limiting the flower head density of the leguminous plant aphids feed on (Bennie et al. 2015a; Sanders et al. 2015). Additionally, it also appears to increase the relative abundance of predatory and scavenging species in insect communities exposed to artificial lighting, probably because of an increase in the number of insect cadavers accumulating under streetlights (Heiling 1999; Davies et al. 2012). Consequently, the cascading effects of artificial lighting on biological communities may have profound impacts on ecosystem functions such as pest control, pollination, and seed dispersal. As an example, moths at the vicinity of streetlights appear to be attracted upward near lamps and away from field margin, and to carry less pollen than their counterparts in dark areas (Macgregor et al. 2016). This suggests that the disruptive effect of artificial lighting on moths may have important impacts on the reproduction of insect-pollinated plant species (Macgregor et al. 2015). Similarly, the artificial illumination of tropical forest

patches in Costa-Rica significantly inhibits the foraging and commuting activity of fruit-eating bats, and likely reduces seed-dispersal across human-inhabited landscapes, where urban sprawl surrounds pristine forest remnants (Lewanzik & Voigt 2014).

Overall, although evidence is lacking on the long-term impacts of artificial lighting on the spatiotemporal dynamics of populations and biological communities, existing scientific literature tends to show that light pollution impacts all levels of organization of ecosystems from the physiology of individuals to the dynamics of biological communities. In this context, these impacts on biodiversity may cumulate with the impacts of land-use changes such as agricultural intensification and urbanization, and hence exacerbate the pressures that are already threatening biodiversity worldwide. However, there are at the moment no artificial lighting regulations in land-use planning to minimize the impacts of light pollution on biodiversity and ecosystem functions, although they may be essential to ensure effective conservation of biodiversity and ecosystem functionality in human-inhabited landscapes (Marcantonio et al. 2015). Furthermore, we are currently at an important crossroad in lighting management, as lighting equipment is reaching its end-of-life in developed countries and is expanding in developing countries. In this context, it appears of major importance to determine and characterize the artificial lighting parameters that can be controlled to mitigate the adverse impacts of outdoor lighting on biodiversity.

3. Levers of actions to limit light pollution impacts

Streetlights along roads, pavements and streets are the most important sources of light pollution. They represent 38% of brightly lit areas in Birmingham (Hale et al. 2013), and 31.6 % of zenith directed light pollution in Berlin (Kuechly et al. 2012). Most of the studies so far investigating the effects of nighttime artificial lighting on biodiversity have focused on the effects of the type of streetlamps (defined by its spectrum; Box 2; Figure 4; Table 2) on physiological and behavioral responses of organisms. In the European Union, the most common types of streetlamps used 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 (EC, 2011). However, since the European Eco-Design Directive (245/2009), HPM lamps are being progressively phased out from the market because of their low energetic efficiency (Table 2). This change occurs concomitantly with the increased cost-effectiveness of energy-efficient Light Emitting Diodes (LEDs), representing so far approximately 7 % of the European market (Zissis & Bertoldi 2014). HPM, MH and standard white-LEDs lamps have broad-spectrum emissions, with an important peak of energy in the blue range (Correlated Color Temperature (CCT) > 3000 K; Figure 4; Table 2). HPS lamps also have broad-spectrum emissions although they present an important peak of energy in the orange-red range (CCT < 2700 K; Figure 4; Table 2). In contrast, LPS are narrow-spectrum emitting lamps with a single peak of energy emitted in the yellow range (CCT = 1807 K; Table 2). HPM, MH and HPS lamps emit energy in the UV range (although HPS emit relatively less UVs than HPM and MH), contrary to LEDs and LPS lamps.

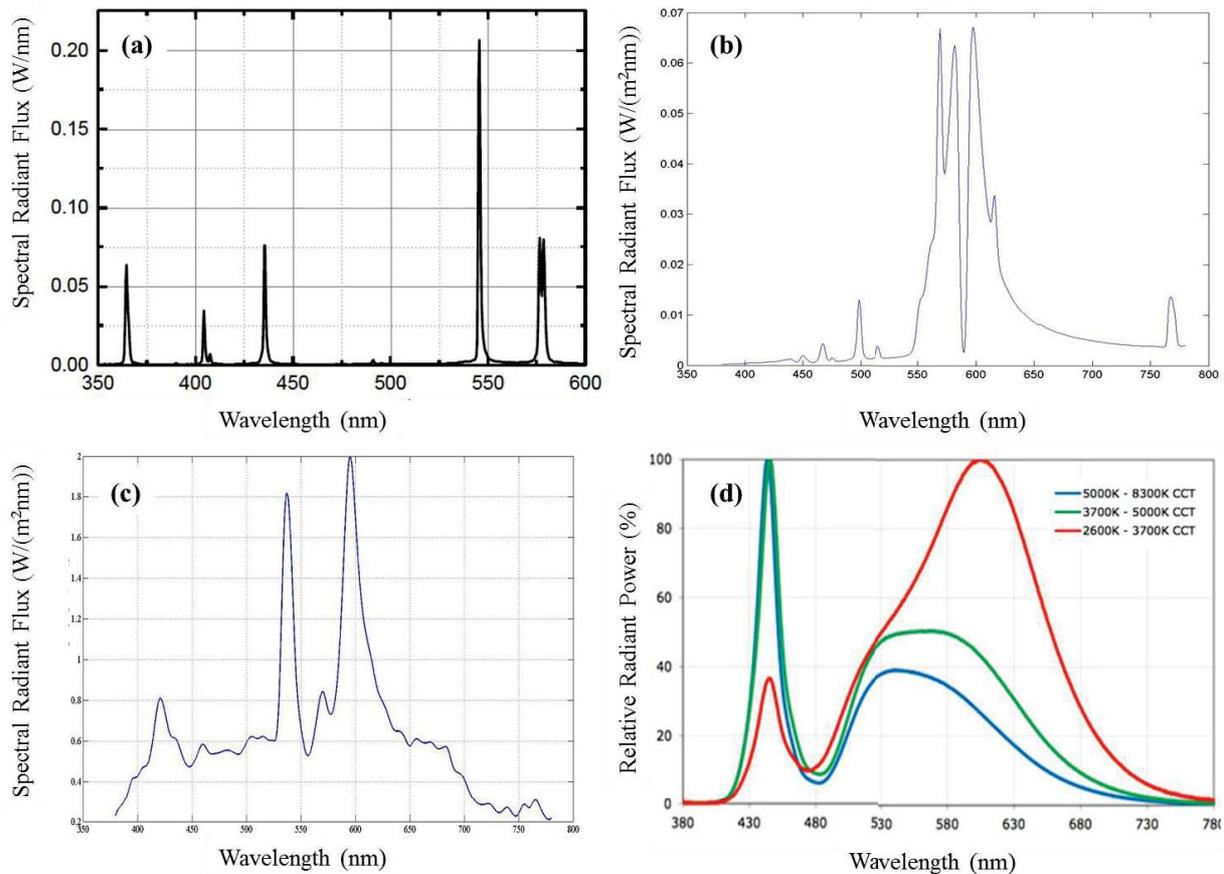


Figure 4. Spectrum of (a) High Pressure Mercury lamps, (b) High Pressure Sodium lamps, (c) Metal-Halide lamps, and (d) Light Emitting Diodes of Correlated Color Temperatures (CCT; Box 1) of 2600-3700 K (red; warm-white lamps), 3700-5000 K (green, “cold-white “ lamps), 5000-8300 K (blue, “cold-white “ lamps). These data come from personal measurements of the Pr. G. Zissis from the Laplace Institute of the Paul-Sabatier University (Toulouse, France) from lamps of 250 W for (a) and 150 W for (b), (c) and (d).

Table 2. Description of the percentage of most common lamps sold in the EU from 2004 to 2007 (EC 2011) as well as their physical characteristics extracted from Gaston al. (2010) and from personal data of Pr. Zissis. CCT refers to Correlated Color Temperature (Kelvin); LE refers to Luminous Efficacy (lumens/W); CRI refers to Color Rendering Index (Definitions in Box 2).

Spectrum	Types of lamps	% sales	Color	UV	CCT	LE	CRI
Narrow	Low Pressure Sodium		Yellow	0	1807	80-150	NA
Broad	High Pressure Sodium	37	Orange/white	+	2005-2108	45-110	22-80
Broad	High/low Pressure Mercury	27	White	++	2766-5193	25-52	22-43
Broad	Metal-Halide	36	White	++	2874-4160	45-150	65-95
Broad	Light Emitting Diode	NA	White	0	1739-8357	160	>90

Box 2. Definition of lamps parameters (inspired from Stone et al. 2013)

Visible spectrum: Part of the electromagnetic spectrum (composed of electromagnetic radiation, *i.e.* photons) that is visible to the human eye. It is composed of wavelength from 300 nanometers (purple) to 700 nanometers (red).

Correlated Color Temperature (CCT): Indication of the color appearance of a light source. CCT < 2700 K refers to “warm” light sources with an important content of long wavelength (orange-red), while CCT > 3000 K refers to “cold” light sources with an important content of short wavelength (blue). CCT is measured in Kelvin (K).

Color Rendering Index (CRI): Indication of the ability of a lamp to reproduce colors. The closer it is from 100, the better it reproduces natural light.

Luminous flux: Rate at which light is emitted from a light source at a given angle (measured in lumens).

Luminous Efficacy: Amount of energy needed to produce visible light (lumens/Watt).

Illuminance: Amount of the luminous flux received by horizontal or vertical planes (measured in lux). As an example, full-moon illuminance is between 0.3 and 1 lx, while daylight at noon is > 20 000 lx during a clear day.

Light trespass: Spill of artificial light in areas that are not intended to be lit.

Low wavelength emissions in the blue and UV ranges raise particular environmental concerns as they control melatonin secretions in animals including humans (Thapan et al. 2001; Brüning et al. 2016), and are responsible for the “flight-to-light” behavior of insects (van Langevelde et al. 2011). In this context, HPM and MH lamps are the most attractive lamps to insects because of their blue and UV contents (Blake et al. 1994; Eisenbeis 2006). Yet, even if LEDs and HPS lamps are less harmful to insects than HPM and MH, white-LEDs still attract 48 % more insects than HPS lamps (Pawson & Bader 2014), and HPS lamps still attract 27 times more insects than under dark conditions (Perkin et al. 2014b). Unsurprisingly, insect predators that have the ability

to exploit illuminated niches, such as fast-flying bats, appear to follow the same pattern of responses. For example, the activity of pipistrelles bats *Pipistrellus sp.* at the vicinity of MH and HPM lamps is significantly more important than under sodium lamps and white-LEDs respectively (Figure 5; Stone et al. 2015b; Lewanzik & Voigt 2016).

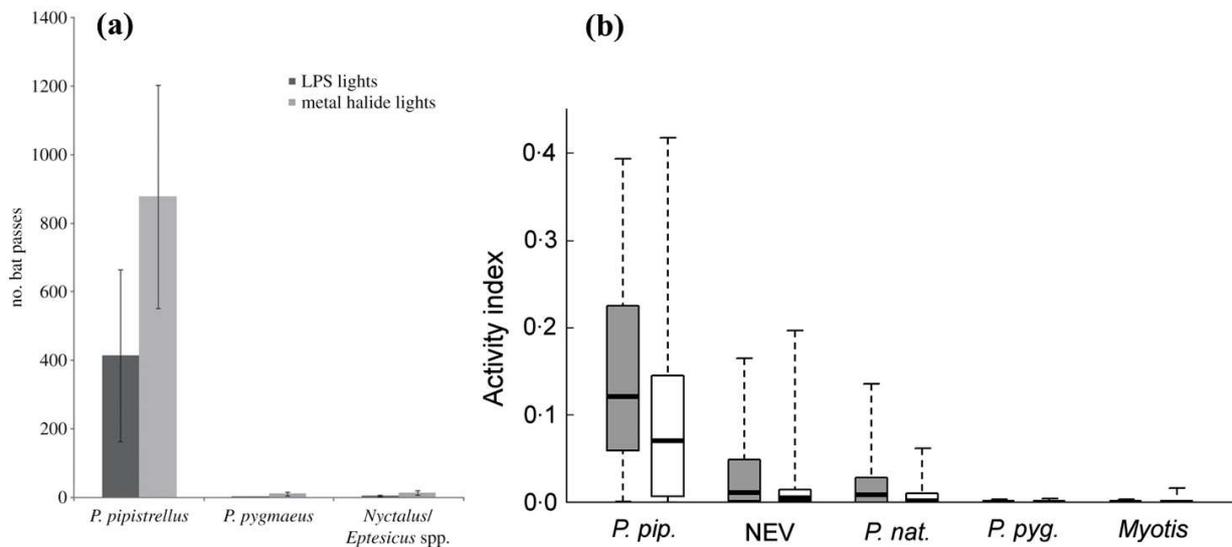


Figure 5. (a) Extracted from Stone et al. (2015) showing the mean bat activity (number of bat passes) of *P. pipistrellus*, *P. pygmaeus* and *Nyctalus/ Eptesicus spp.* at experimental sites before (LPS lights) and after light changeover (metal halide lights); **(b)** Extracted from Lewanzik & Voigt (2016) showing boxplot of bat activity index at MHP (grey, n = 21) and LEDs (white; n = 25) for *P. pipistrellus* (*P. pip.*), *Nyctalus/Eptesicus/Vespertilio spp.* (NEV), *P. nathusii* (*P. nat.*), *P. pygmaeus* (*P. pyg.*) and *Myotis spp.* (*Myotis*). The activity index was calculated by dividing the number of minutes with activity by the 210 min recorded until 3 to 5 hours after sunset .

In contrast, plants respond to higher wavelength emissions in the orange and red ranges. The exposure to amber-LEDs or LPS lighting decreases the flower head density of leguminous plants with cascading impacts on the density of insect herbivore populations (Bennie et al. 2015a). Additionally, the avoidance behavior of some light-sensitive species such as the lesser horseshoe bat *R. hipposideros* and the wood mice *Apodemus sylvaticus* persist regardless of the lamp spectrum tested (Stone et al. 2009, 2012; Spoelstra et al. 2015). Nighttime artificial lighting also appears to inhibit mating in a geometrid moth regardless of the color spectrum (van Geffen et al.

2015b). In this context, it is quite unlikely to find a lamp spectrum that has the ability to simultaneously limit the different adverse impacts of nighttime artificial lighting on biodiversity as a whole.

Dimming outdoor lighting to limit the illuminance (defined in Box 2) received by areas surrounding streetlights may be an interesting option to limit the spatial extent of lighting and avoid light trespass in areas that are not intended to be lit (Kyba & Hölker 2013; Gaston et al. 2015; Marcantonio et al. 2015). However, the adverse impacts of nighttime artificial lighting on the circadian and seasonal rhythms of diurnal passerine birds were detected at illuminance values lower than 0.3 lx (Figure 6; Dominoni et al. 2013b; de Jong et al. 2016). This suggests that even small changes in natural light regime may have profound impacts on biodiversity. Thus, the enhancement and conservation of dark refuge and dark ecological corridors without any source of artificial lighting appear to be a key issue to effectively mitigate the impacts of nighttime artificial lighting on biodiversity.

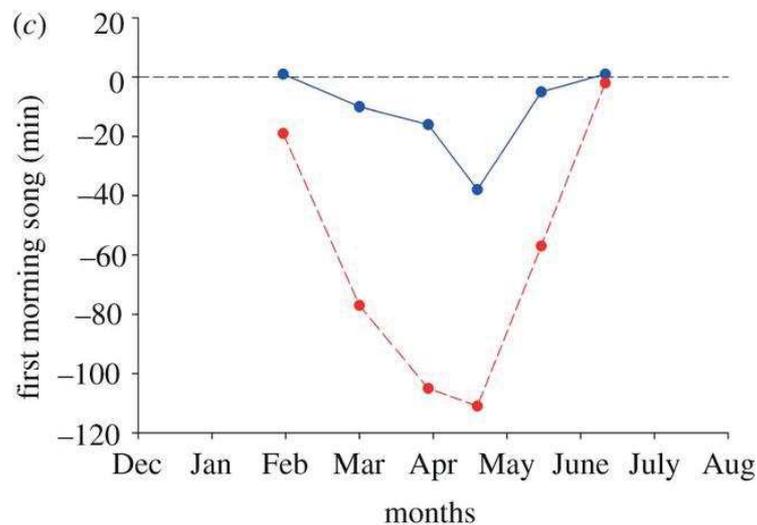


Figure 6. Extracted from Dominoni et al. (2013b) showing the time of first morning song in adult male European blackbirds (*Turdus merula*) captured in rural areas and kept in laboratory. European blackbirds were tested to simulated natural photoperiods but with different light intensities at night. Control birds (blue) experienced nights without any light, whereas experimental birds (red) were exposed to constant light of 0.3 lux at night.

In this context, limiting the temporal and spatial extents of lighting may be the best option to effectively restore darkness both in time and in space in human-inhabited landscapes (Kyba et al. 2014b). Thus, outdoor lighting planning requires to manage nighttime artificial lighting through 5 integrated levers of action that first emphasize **1) the spatial arrangement of artificial light sources** in the landscape and **2) its duration** (Kyba et al. 2014b). Second, once areas and time periods that actually need to be lit have been defined, it should focus on **3) the reduction of light trespass** through precise directionality of the luminous flux; **4) the reduction in the illuminance** emitted by light sources; and **5) the adaptation of the spectral composition** of the lamps according to the ecological context (Gaston et al. 2012).

4. “Knowledge gaps” and plan of the thesis

Most of the studies on the impacts of nighttime artificial lighting on biodiversity have been set up at local scales through experimental designs and have investigated the impacts of one or several streetlights on species physiology and behavior. They revealed the dramatic impacts of artificial lighting on species rhythms of activity and movements. They suggest that light pollution may generate important costs for populations in the long-term as it likely decreases individual fitness and reproductive success, increases mortality and limits movements and dispersal (Table 1). Nevertheless, no study has actually investigated the long-term effects of light pollution on the temporal trends and the spatial distributions of populations, and evidence is lacking on whether this phenomena is negligible compared to the adverse impacts of global changes on biodiversity. This is however crucial to hierarchize biodiversity threats and conservation actions, and to elaborate effective land-use planning strategies. In this context, in the first chapter of my PhD, I intended to characterize the impacts of light pollution on bat activity and occurrence at a landscape scale (See Box 3 for details on the use of bats as model species). Landscape-scale

studies allow to infer the long-term consequences of a given environmental factor on populations because this approach focus on population-scale responses **between different landscapes** (e.g. abundance, spatial distribution), contrary to local-scale studies that focus on behavioral response of individuals to an environmental factor **in a given landscape** (e.g. movements, activity rhythms ; Fahrig 2003). Using the national-scale citizen science database from the French bat monitoring program “Vigie Chiro”, I intended to answer the 2 following questions:

- **What are the landscape-scale effects of light pollution on bat activity and occurrence?**
- **What is the relative effect of light pollution compared to the effects of urbanization (in terms of impervious surfaces) and of intensive agriculture?** These land-use changes are the 2 main drivers of global biodiversity loss worldwide as they generate major habitat loss, fragmentation and degradation (Donald et al. 2001; Eigenbrod et al. 2011).

This study has been published in *Landscape Ecology* in 2016:

- **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*. DOI:10.1007/s10980-016-0417-3.

Second, although many studies investigated the impacts of the lamp spectrum and illuminance on biodiversity, evidence is lacking on **the effects of the duration and the position of street lighting** even if it is determinant for the enhancement **dark refuges** in human-inhabited landscapes (i.e. levers of actions 1 and 2). These 2 aspects are major issues in land-use planning as current policies tend to restore biodiversity dynamics in human-inhabited landscapes by

enhancing functional networks of ecological corridors. However, there is at the moment no recommendation for nighttime artificial lighting management in and around these areas of ecological importance.

Thus, in the second chapter of my PhD, I investigated the effect of outdoor lighting management measures that aimed at **limiting the temporal extent of artificial lighting**, and hence at restoring darkness in a landscape for a part of the night, on bat activity. Following the major economic crisis of 2008 and the subsequent dramatic increase in the costs of energy, many local administrations launched part-night lighting schemes designed for turning-off public streetlights from midnight to 05 AM approximately. However, the effectiveness of this measure in limiting the negative impacts of artificial lighting on biodiversity is unknown. Thus, I designed an *in situ* experiment to answer the following question:

- **Can current part-night lighting schemes effectively limit the impacts of outdoor lighting on bat activity?**

The results of this experiment were published in *Global Change Biology* in 2015:

- Azam C, Kerbiriou C, Vernet A, Julien JF, 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* 21:4333–4341.

Finally, in the third chapter of my PhD, I focused on the **spatial distribution of artificial lighting** in human-inhabited landscapes. In particular, I focus on how the position of streetlights relative to ecological corridors affected bat activity. I intended to elaborate outdoor lighting recommendations that can effectively **limit the spatial extent of artificial lighting** at the vicinity of ecological corridors, and hence allow their use by light-sensitive nocturnal species. Using the same experiment set up as in chapter 2, I intended to answer the following questions:

- **What is the distance of impact of streetlights on bat activity?**
- **Is there a threshold of impact of light illuminance on bat activity?**
- **Do these effects persist once streetlights are turned off?**

This study will be submitted for publication before December 2016:

- Azam C, Le Viol I, Bas Y, Zisis G, Vernet A, Julien JF, Kerbiriou C. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity.

Box 3. Using microchiropteran bats as model species (Jones et al. 2009)

- ✓ **Nocturnal** => Directly exposed to light pollution
- ✓ **Often roost in buildings and human settlements and hence can exploit human-inhabited landscapes** => Directly exposed to light pollution
- ✓ **High trophic level** => Changes in abundance may reflect changes in arthropods preys
- ✓ **Slow reproductive rate** => Important sensitivity to climate and land-use changes

- ✓ **Large-scale standardized sampling** => Emergence of automatic acoustic recording tools

CHAPTER 1:

Characterization of the landscape-scale effects of light pollution on bat activity relative to other land-use pressures in France

Based on the publication :

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*. DOI:10.1007/s10980-016-0417-3

Introduction

Land-use changes induced by the intensification of agriculture and the dramatic development of urban infrastructures, generate large scale loss and fragmentation of natural habitats and is responsible for major biodiversity decline worldwide (Donald et al. 2001; Eigenbrod et al. 2011; Penone et al. 2013). However, the extent of effect of light pollution in this context of global changes is unknown, although it appears to be essential to hierarchize biodiversity threats and design sustainable land-use planning strategies. Thus, in the present chapter, we intended to characterize the patterns of response of 4 common bat species to landscape-scale level of light pollution in France using a national-scale citizen science database. Because of their large spatial distribution and their relative abundance, common species are particularly valuable model species to monitor the impacts of global changes on biodiversity over large spatial and temporal scales (Devictor et al. 2010; Jiguet et al. 2012). Furthermore, they are of major importance for ecosystem structure as they represent the most important number of individuals in a biological community, and the major part of ecosystem biomass and energy turnover (Gaston & Fuller 2008; Gaston 2010). National-scale citizen science monitoring programs provide valuable insights to measure ongoing population declines of common species over large spatial scales, and to predict current and future species distribution under different human development scenarios (Sala et al. 2000; Clavel et al. 2011; Le Viol et al. 2012). In this context, we coupled the use of national citizen-science database with a new generation of nighttime light satellite data **to characterize the effect of light pollution at 4 different landscape scales** on the activity and occurrence of 4 common species of bats, and **to compare its relative effect compared to intensive agriculture and impervious surface**.

Disentangling the relative effect of light pollution, impervious surfaces and intensive agriculture on bat activity with a national-scale monitoring program

Clémentine Azam · Isabelle Le Viol · Jean-François Julien · Yves Bas · Christian Kerbiriou

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Abstract

Context Light pollution is a global change affecting a major proportion of global land surface. Although the impacts of Artificial Light At Night (ALAN) have been documented locally for many taxa, the extent of effect of ALAN at a landscape scale on biodiversity is unknown.

Objectives We characterized the landscape-scale impacts of ALAN on 4 insectivorous bat species *Pipistrellus pipistrellus*, *Pipistrellus kuhlii*, *Eptesicus serotinus*, *Nyctalus leisleri*, and compared the extent of their effects to other major land-use pressures.

Methods We used a French national-scale monitoring program recording bat activity among 2-km car transect surveys, and extracted landscape characteristics around transects with satellite and land cover layers. For each species, we performed multi-model averaging at 4 landscape scales (from 200 to 1000 m buffers around transects) to compare the relative effects of the average radiance, the proportion of

impervious surface and the proportion of intensive agriculture.

Results For all species, ALAN had a stronger negative effect than impervious surface at the 4 landscape scales tested. This effect was weaker than the effect of intensive agriculture. The negative effect of ALAN was significant for *P. pipistrellus*, *P. kuhlii* and *E. serotinus*, but not for *N. leisleri*. The effect of impervious surface varied among species while intensive agriculture had a significant negative effect on the 4 species.

Conclusion Our results highlight the need to consider the impacts of ALAN on biodiversity in land-use planning and suggest that using only impervious surface as a proxy for urbanization may lead to underestimated impacts on biodiversity.

Keywords Outdoor lighting · Urbanization · Land-use planning · Nightscape · Bats · Chiroptera

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C. Azam (✉) · I. Le Viol · J.-F. Julien · Y. Bas · C. Kerbiriou
Center for Ecology and Conservation Science, UMR7204-MNHN-CNRS-UPMC, National Natural History Museum, 55 rue Buffon, 75005 Paris, France
e-mail: cazam@mnhn.fr

Introduction

Land-use changes, mostly agricultural intensification and urbanization, are considered as major drivers of global biodiversity loss (Foley et al. 2005). The habitat loss and fragmentation they induce have been associated globally to species decline (Donald et al. 2001; Tilman et al. 2001; Penone et al. 2013), large scale biotic homogenization (Devictor et al. 2007; Le Viol

et al. 2012) and loss of ecosystem services (Kremen et al. 2002; Deguines et al. 2014). However, these land-use changes also generate different types of pollution such as chemical, noise and artificial light (Forman and Alexander 1998; Grimm et al. 2008; Kyba and Hölker 2013), whose extent of effect on biodiversity has not always been assessed (Grimm et al. 2008). In particular, Artificial Light At Night (ALAN) is an urban-induced pollution that affects a substantial part of world (Falchi et al. 2016) and that is increasing on average by 6 % per annum worldwide (Hölker et al. 2010).

The alteration of natural light cycles induced by the widespread use of ALAN has major impacts on the biological rhythms of both nocturnal and diurnal organisms (Gaston et al. 2014). The subsequent desynchronization of population rhythms of activity with their environment generates important costs for the fitness of individuals from a wide range of taxa such as birds, insects and bats (Boldogh et al. 2007; Nordt and Klenke 2013; Da Silva et al. 2015; Van Geffen et al. 2015; Robert et al. 2015). Furthermore, the response of species to ALAN are driven by attraction/repulsion behaviors, so the movements and distribution of species can be shifted at multiple spatial scales (Stone et al. 2009, 2012; Mathews et al. 2015). Taken together, the effects of ALAN on organisms likely disrupt the spatiotemporal dynamics of biological communities and ecosystems (Bennie et al. 2015; Davies et al. 2015; Minnaar et al. 2015; Sanders et al. 2015).

So far, studies on the effects of ALAN on biodiversity have mostly been set up at local scales, focusing on physiological and behavioral responses of organisms to one or several streetlights (Rich and Longcore 2006; Stone et al. 2012; Perkin et al. 2014; de Jong et al. 2015). However, the landscape-scale impacts of ALAN on biodiversity are unknown (Kyba and Hölker 2013) although essential to infer its long-term consequences on population dynamics (Gaston and Bennie 2014). In fact, it is of major importance to characterize the relative contribution of ALAN to the habitat loss and fragmentation generated by land-use changes to address sustainable land-use planning strategies (Grimm et al. 2008; Gaston et al. 2014).

Particularly sensitive to habitat loss and fragmentation and increasingly threatened worldwide (Mickelburgh et al. 2002), bats are suitable model species to

compare the effects of ALAN relative to other land-use pressures. As long-lived insectivorous species with a slow reproductive rate, microchiropteran bats are considered to be good indicators of the response of biodiversity to anthropogenic pressure (Jones et al. 2009). Furthermore, several studies have pointed to their value in providing ecosystem services such as pest control (Cleveland et al. 2006; Charbonnier et al. 2014).

Bat activity and occurrence are known to be negatively affected by increased urbanization (Hale et al. 2012; Jung and Threlfall 2016) as well as agricultural intensification (Wickramasinghe et al. 2003; Jennings and Pocock 2009). However, the responses of bats to ALAN at a landscape scale are unclear. At a local scale, bat responses to ALAN vary among species according to their foraging strategy and flight abilities (Jones and Rydell 1994). Slow-flying species adapted to prey on insects in cluttered vegetation, such as *Rhinolophus spp.* and *Myotis spp.*, are more likely to be affected by illuminance (Rydell 1992; Stone et al. 2009, 2012; Kuijper et al. 2008; Azam et al. 2015) due to an intrinsic preception of increased predation risk (Jones and Rydell 1994; Rydell et al. 1996). In contrast, fast-flying species adapted to hunt insects at dusk in the open air, such as *Pipistrellus spp.* and *Nyctalus spp.*, can benefit from new and predictable foraging opportunities provided by streetlights (Rydell 1992; Blake et al. 1994; Lacoëuilhe et al. 2014; Azam et al. 2015), which attract a large proportion of the surrounding flying insect biomass (Perkin et al. 2014). In this context, ALAN is likely to be a driver of habitat loss and fragmentation for slow-flying species while creating new and predictable foraging opportunities in the landscape for fast-flying species (Stone et al. 2012; Lacoëuilhe et al. 2014; Azam et al. 2015).

However, movements and gap-crossing behaviors of fast-flying species can also be altered by ALAN in urban landscapes (Hale et al. 2015), suggesting that an increase in landscape-scale level of ALAN may reduce landscape connectivity for all species regardless of their foraging strategy. Such an increase may also reduce the availability of suitable dark roosting sites in the landscape although essential for the reproduction of all bat species (Boldogh et al. 2007). Overall, landscape-scale level of ALAN may significantly change the spatial dynamics of bat species at multiple spatial scales, although evidence is lacking as

to whether its potential benefits for some species outweigh its costs.

In this study, using a French national-scale citizen-science database, we aimed to (i) characterize the effects of ALAN on bat activity and probability of presence at 4 different landscape scales and (ii) compare the relative effect of ALAN to other land-use effects with a particular emphasis on the effects of the proportion of impervious surfaces and of intensive agriculture. Our goal was to determine whether the extent of effect of ALAN is significant at a landscape-scale relative to land-use pressures that are considered as major threats for biodiversity (Foley et al. 2005).

Materials and methods

Car transect survey

The data were provided by the French bat-monitoring program (<http://vigienature.mnhn.fr/page/vigie-chiro>), a citizen-science program running since 2006 and coordinated by the French National Museum of Natural History (NMNH). Volunteer surveyors recorded bat activity while driving at a constant low-speed (25 ± 5 km/h) along a 30 km road circuit within a 10 km buffer around their home (Fig. 1). Surveyors were asked to design their road circuit so that it proportionally crossed the different land-cover types and it remained on low-traffic roads for security reasons. After final validation of the circuit outline, program coordinators randomly selected the starting point of the survey. Each circuit was then divided into 10×2 km transects where bat were recorded, separated by 1 km road portions where recording was not carried out (Fig. 1b).

We used data from surveys carried out every year from the 15th of June to the 31st of July, corresponding to a seasonal peak in bat activity. Surveys started 30 min after sunset and lasted approximately 1.5 h during the period of bat activity. They were only carried out when weather conditions were favorable (i.e., no rain, low wind speed of <7 m/s, temperature >12 °C). We obtained a total of 160 road circuits representing 1610 different transects (Fig. 1a) where coverage was largely representative of French land-cover (Table 1). As 56 % of transects were sampled for several years by surveyors (maximum = 6 years), we had 3996 transects replicates for the analyses.

Biological data

Along transects, volunteer surveyors recorded bat echolocation calls with ultrasound detectors connected to a Zoom H2 digital recorder (Samson technologies, USA) and reported the date of survey and temperature (°C). Sound was stored on Secured Card in Waveform Audio File Format, more commonly known as WAV format. The ultrasound detectors used by surveyors were either Tranquility Transect (Courtpan Design Ltd, UK) or D240X (Pettersson Elektronik, Sweden). As the 2 devices did not have the same record length, we applied a correction on the acoustic recordings of D240X to be able to compare the data obtained from both devices (See Table S1 and S2 for details). After a 2-day training course, surveyors classified all the echolocation calls to the most accurate taxonomic level using Syrinx 2.6 (Burt 2006), and applied an identification confidence index to each of their recordings (0 when they were not sure, and 1 when they were sure of their identification). Data validation was then manually done by NMNH experts for recordings with a 0-confidence index (Table S1). We used data from 2006 to 2013 representing a total of 23610 bat passes. We conducted the analysis on *Pipistrellus pipistrellus* ($n = 15355$), *Eptesicus serotinus* ($n = 2652$), *Pipistrellus kuhlii* ($n = 2319$), which may include 8 % of *P. nathusius* (See Table S1 for details) and *Nyctalus leisleri* ($n = 2052$). The first species represented 65 % of the dataset while the 3 others represented approximately 10 %.

Landscape characteristics

Around each of the 1610 transects, we generated a set of landscape variables calculated within 4 different landscape buffers of 200, 500, 700 and 1000 m using ArcGIS 10.2. We used radiance as a measure of ALAN as it is defined as the radiant flux (i.e., radiant power) reflected or emitted by a given surface. We used the VIIRS nighttime lights (2012) which is a 2-months composite raster of radiance data (in nW/cm^{-2} sr) collected by the Suomi NPP-VIIRS Day/Night Band during 2 time-periods in 2012 (20 nights in total) on cloud-free nights with zero moonlight (Baugh et al. 2013). We then computed the average radiance within each buffer with the tool “Zonal

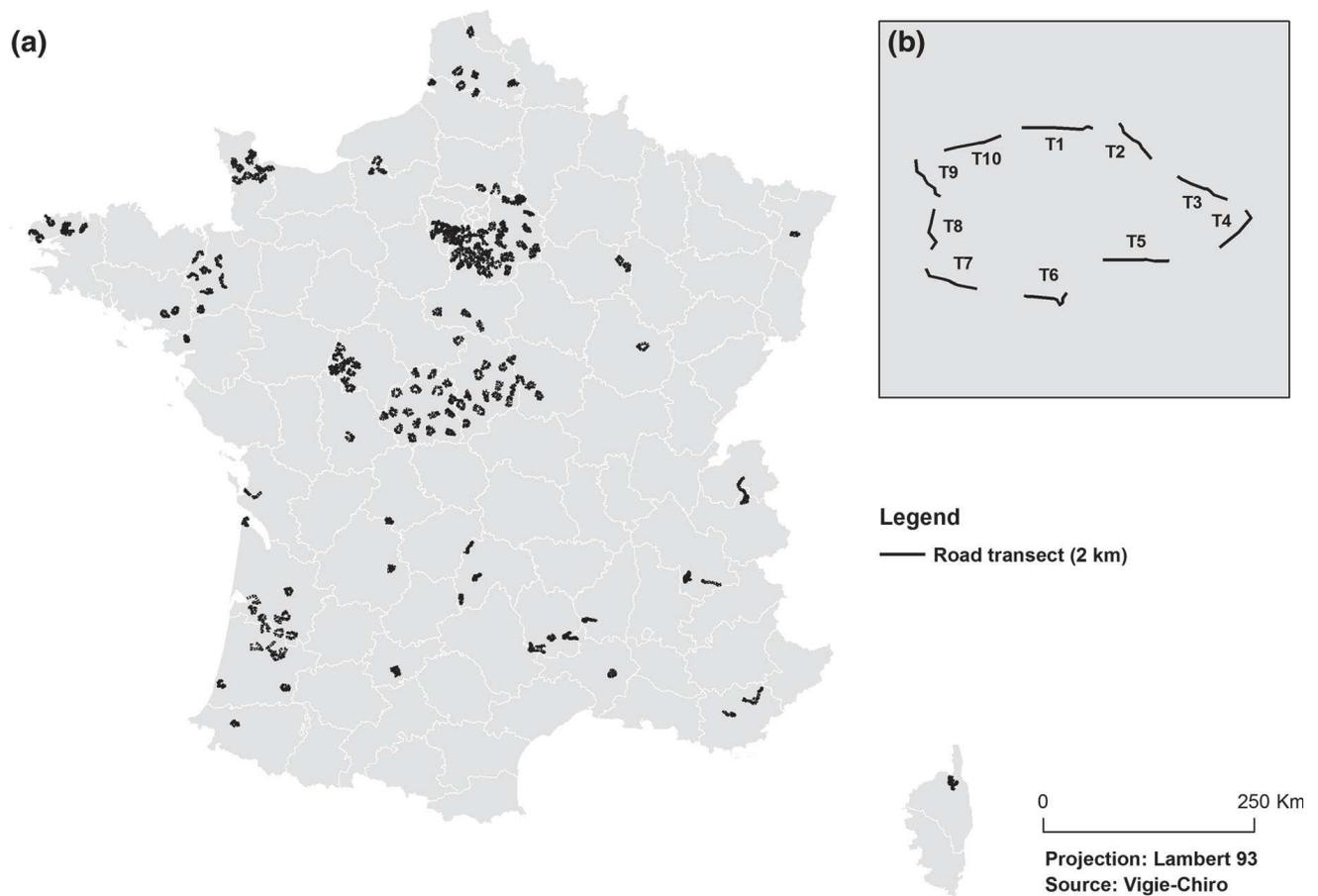


Fig. 1 Map of the distribution in France of the 160 road circuits from the French Bat Monitoring Program (a) and example of one road circuit composed of 10 transects named T1–T10 (b).

Table 1 The land-cover variables surrounding each transect at a range of spatial scales (200–1000 m), as well as their representativeness in mainland France

Landscape variables	Mainland France	Transects (200 m)	Transects (500 m)	Transects (700 m)	Transects (1000 m)	Range (min–max)
Av. radiance (nW/cm ⁻² sr)	3.2	2.21	2.15	2.08	2.07	0.1–55.5
Imper. surf. (%)	5.2	11.3	8.74	7.3	6.5	0–92
Inten. agri. (%)	28.1	32.5	34.0	34.3	34.9	0–100
Exten. agri. (%)	11.0	12.9	11.5	11.8	11.4	0–92
Forests (%)	19.9	18.6	24.7	20.7	21.2	0–100
Roads (m/ha)	1.92	12.8	6.8	5.4	4.3	0–9391
Streams (m/ha)	6.67	12.9	10.5	9.8	9.1	0–22262

The variables are the average radiance, the proportions of impervious surface, intensive agriculture, extensive agriculture, forests, and mean length per hectare of roads and streams. The range represents the minimum and the maximum values encountered for each variable around transects at 1000 m landscape-scale (similar range were observed for the 3 other landscape scales tested)

statistics as Table” from the package “Spatial Analyst” (See Fig. S1 for details).

We calculated the proportion (%) of impervious surface (Code 1.1 (consisting of 99 % of Code 1.1.2);

CORINE Land Cover/2006) and the proportion of intensive agriculture (Code 2.1; CORINE Land Cover/2006) within each buffer as they represented major land-use pressures. The proportion of

impervious surface included buildings and pavement (roads, sidewalks, driveways and parking lots) that are covered by impenetrable materials such as asphalt, concrete, brick and stone. The proportion of intensive agriculture included irrigated and non-irrigated arable land such as cereals, leguminous and forage crops. The effect of road network which can also be considered as a land-use pressure (especially regarding landscape connectivity) could not be tested in our study because transects were mostly located in areas with secondary low-traffic roads. For this reason, we only took into account the total length of roads (IGN/2012) within each buffer as a potential confounding factor of the average luminance and the proportion of impervious surface. We also used as covariables: (i) the proportion of extensive agriculture, defined as areas with a complex mosaic of annual and permanent cultures and semi-natural habitats (Code 2.4; CORINE Land Cover/2006); (ii) the total length of streams and water sources (IGN/2012); and (iii) the proportion of deciduous and mixed forests (Code 3.1; CORINE Land Cover/2006) as they were commonly represented in our buffers and were known to influence bat activity at a landscape scale (Boughey et al. 2011; Frey-Ehrenbold et al. 2013; Fonderflick et al. 2015). Only the proportion of impervious surface and the average radiance were highly correlated at the 4 landscape scales tested ($r > 0.7$, Table S3). We did not have multicollinearity problems in models when we excluded one of these 2 highly correlated variables (Variance Inflation Factor < 2 ; Fox and Monette 1992). At 1000 m landscape scale, there was 25 % overlap between nearby transects belonging to a same road circuit. However, this still allowed the measurement of variation in landscape characteristics within the same road circuit. However, we could not go into larger landscape scales as the overlapping rate between transect buffers would exceed 50 %.

Statistical analyses

We applied generalized linear mixed models using as a response variable the number of bat passes per transect with a Poisson error distribution for *P. pipistrellus*, and the presence/absence of species per transect with a Binomial distribution for *P. kuhlii*, *E. serotinus*, and *N. leisleri* (See Fig. S2 for details). The 7 landscape variables as well as the date of survey and the temperature were used as fixed effects whereas road

circuit name and the year of survey were used as 2 independent random effects. The 9 fixed effects were centered and standardized so that the regression coefficients were comparable in magnitude and their effects were biologically interpretable (Schielzeth 2010).

For each species and at each landscape scale, we generated a set of candidate models containing all possible combinations of the 9 fixed effects, except the simultaneous inclusion of the proportion of impervious surface and the average radiance in a same model as they were highly correlated at all landscape scales ($r > 0.7$, Table S2). All explanatory variables were included in 24 models, except for the proportion of impervious surface and the average radiance. These 2 variables were only included in 16 models as they could not be simultaneously included in a same model. For each set of candidate models, we did multi-model inference averaging to obtain a comparable averaged regression coefficient for each fixed effect (Smith et al. 2009; Grueber et al. 2011). The averaged regression coefficient is defined as the mean of all the partial regression coefficients of the models tested, weighted by the Akaike's model weight (Burnham and Anderson 2002).

In addition, for each species and for each of the 4 landscape scales, we selected one single best model with the smallest AIC value to determine which of the 4 landscape scales tested was the most parsimonious (Nally 2000). For each species, models had the same structure at the 4 landscape scales to allow for the comparison of AIC across scales. All the analyses were run under R 3.1.3 with the package "MuMIn" (Barton 2015) and "lme4" (Bates et al. 2015).

Results

For all species, multi-model averaging showed that average radiance had a stronger negative effect than the proportion of impervious surface at the 4 landscape scales considered (Figs. 2, 3). Selection of the best model led to similar results with models with smallest AIC always including average radiance instead of the proportion of impervious surface at the 4 landscape scales for all species except *N. leisleri* (Table 2; Fig. 3). The relative effect of average radiance was however weaker than the effect of the

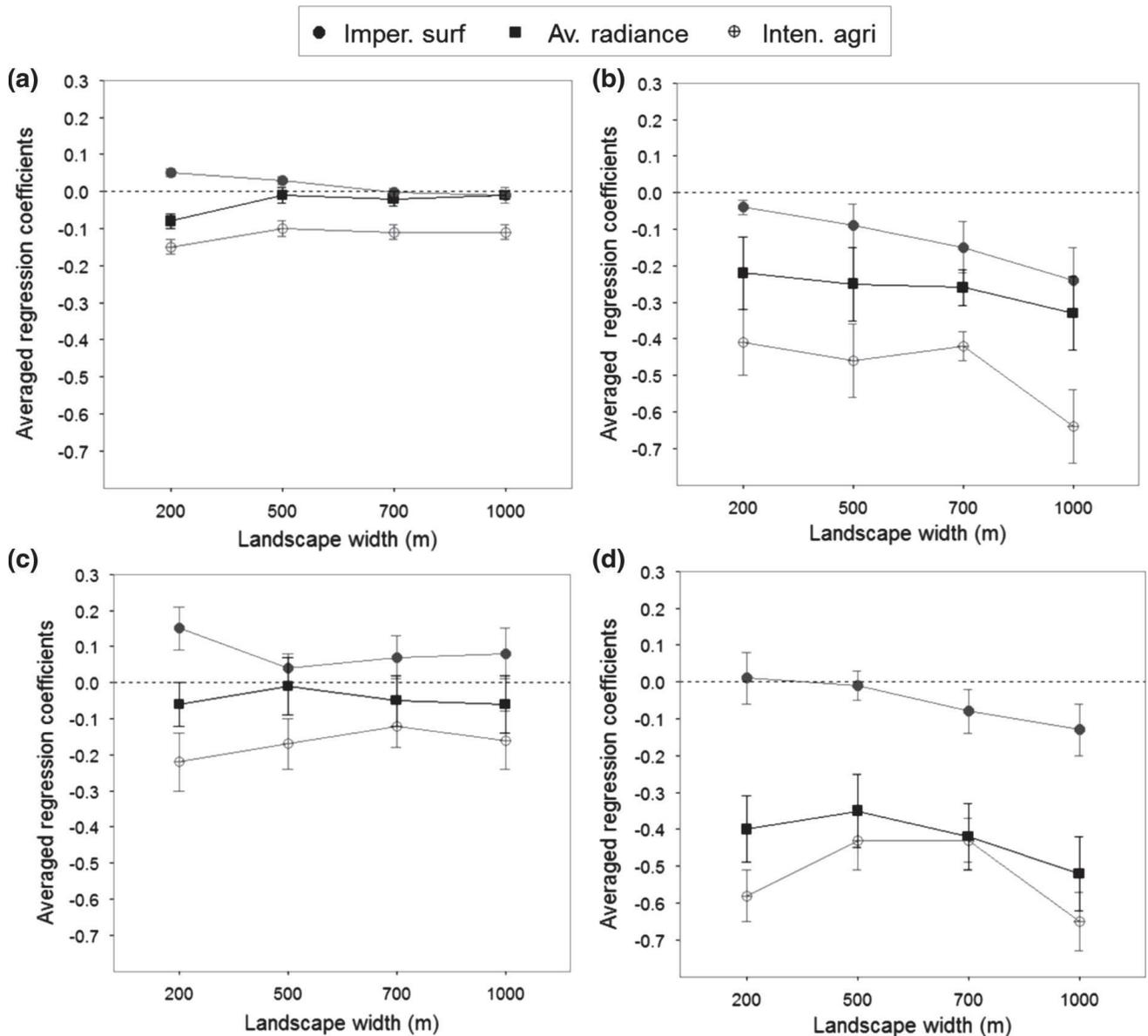


Fig. 2 Averaged standardized partial regression coefficients and associated standard errors from GLMMs model averaging for the average radiance (black squares), the proportion of impervious surfaces (filled grey dots) and the proportion of intensive agriculture (grey empty circles) for *P. pipistrellus* (a),

P. kuhlii (b), *N. leisleri* (c), *E. serotinus* (d) at 200, 500, 700 and 1000 m landscape scales. The 3 landscape variables have a significant effect on species abundance for (a), and probability of presence for (b), (c), and (d), when the error bars of coefficients do not overlap with the 0-horizontal dashed line

proportion of intensive agriculture (Figs. 2, 3) except for *E. serotinus* for which the effects of both landscape variables were of similar extent at 500 and 700 m landscape scales (Fig. 2d).

Average radiance had a significant negative effect on the probability of presence of *P. kuhlii* and *E. Serotinus* at the 4 landscape scales considered and on the activity of *P. pipistrellus* at 200 m landscape scale (Figs. 2, 4; Table S4). In particular,

the activity of *P. kuhlii* appears to dramatically drop after a threshold of radiance value of $0.4 \text{ nW/cm}^{-2} \text{ sr}$ (Fig. 4b). It also had a negative effect on the probability of presence of *N. leisleri* (Fig. 2c), although the effect was not significant (Fig. 4c; Table S4). The effect of the proportion of impervious surface varied among species, with a significant positive effect on the probability of presence of *N. leisleri* and on the activity of *P. pipistrellus* at

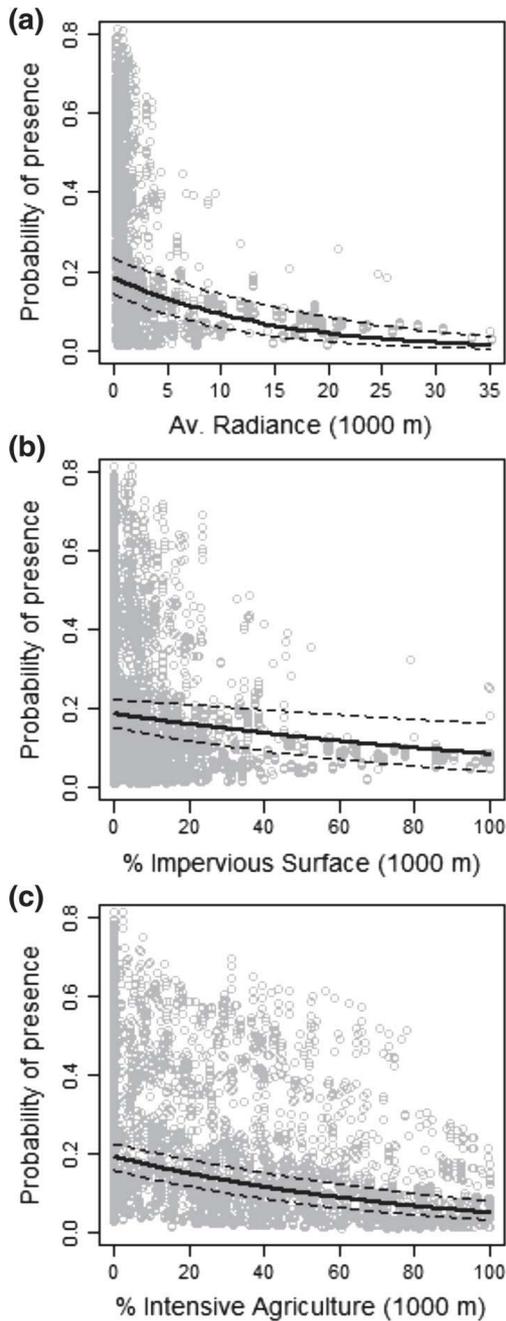


Fig. 3 Relation between *P. kuhlii* predicted probability of presence and the average radiance (a), the proportion of impervious surface (b) and the proportion of intensive agriculture (c) at a 1000 m landscape scale. The solid lines represent the predicted responses obtained with GLMMs and the dashed lines represent the standard errors. Average luminance and impervious surface were tested in 2 separate models which both had the exact same structure and covariables (i.e., Table 2)

200 m landscape scale (Fig. 2a, c; Table S4), and a negative effect on the probability of presence of *P. kuhlii* and *E. serotinus* at the 4 landscape scales

considered (Fig. 2b, d), although only significant at 1000 m landscape scale for *E. serotinus* and at 700 and 1000 m landscape scales for *P. kuhlii* (Fig. 3; Table S3). The proportion of intensive agriculture had a significant negative effect for all species at the 4 landscape scales considered (Figs. 2, 3c; Table 2 and Table S3).

Best model selection showed that the activity of *P. pipistrellus* and the probability of presence of *N. leisleri* were best predicted (smallest AIC) by models that included landscape variables measured at a 200 m landscape scale (Table 2). In contrast, the probability of presence of *E. serotinus* and *P. kuhlii* were best predicted at 500 and 1000 m landscape scale respectively.

Discussion

Our results revealed that ALAN was more strongly associated with a decrease in bat activity and probability of presence than impervious surface for the 4 species studied (Fig. 2). Furthermore, although average radiance and impervious surface were highly correlated at the country-scale, ALAN was always a better predictor of bat activity and occurrence than impervious surface for all species except *N. leisleri* (Table 2). Given that the 4 species studied are the most common bat species in France (Arthur and Lemaire 2009), these results highlight the urgent necessity of taking into account such impacts on biodiversity in urban-planning (Grimm et al. 2008).

The effect of impervious surface was contrasted among the 4 species with a positive effect on *P. pipistrellus* and *N. leisleri*, and a negative effect on *P. kuhlii* and *E. serotinus*. It is however important to note that the positive correlations of impervious surface with species occurrence were significant at a 200 m landscape scale while negative correlations were observed at a 1000 m landscape scale. It has been hypothesized that landscape variables affecting breeding and foraging success have a smaller scale of effect than variables influencing dispersal success (Jackson and Fahrig 2014; Miguet et al. 2015). In this context, the proportion of impervious surface may generate habitat loss and fragmentation at large landscape scale, while providing habitat heterogeneity and complementarity for foraging at a local scale (Jung and Kalko 2010; Jung and Threlfall 2016). Furthermore, most of the car transect surveys were located in

Table 2 Estimated standardized regression coefficients and standard errors (***) $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; $P = \pm 0.05$) from AIC best model selection for the average luminance or the proportion of impervious surface, and the proportion of intensive agriculture for each species and at each of the 4 landscape scales considered.

Species	Scale	Av. luminance	Imper. surf.	Inten. agri.	AIC	Final model formula
<i>P. pipistrellus</i>	NULL	/	/	/	26989	/
	200	-0.08 (0.01)***	/	-0.14 (0.01)***	25252	Av. lum. + Inten. agri. + Forests + Streams + Roads + Date + Temp.
	500	-0.05 (0.01)***	/	-0.13 (0.02)***	25308	
	700	-0.03 (0.01)*	/	-0.12 (0.02)***	25378	
	1000	-0.02 (0.01)	/	-0.11 (0.02)***	25414	
<i>P. kuhlii</i>	NULL	/	/	/	3757	/
	200	-0.22 (0.09)*	/	-0.42 (0.08)***	3308	Av. lum. + Inten. agri. + Exten. agri. + Forests + Streams + Temp.
	500	-0.27 (0.10)**	/	-0.49 (0.09)***	3305	
	700	-0.29 (0.10)**	/	-0.55 (0.09)***	3300	
	1000	-0.32 (0.10)***	/	-0.61 (0.09)***	3289	
<i>N. leisleri</i>	NULL	/	/	/	3431	/
	200	/	0.14 (0.06)*	-0.20 (0.07)**	3204	Imper. surf. + Inten. agri. + Exten. agri. + Streams + Temp.
	500	/	0.03 (0.04)	-0.18 (0.07)**	3215	
	700	/	0.11 (0.06)	-0.14 (0.07)*	3212	
	1000	/	0.07 (0.07)	-0.12 (0.07)	3217	
<i>E. serotinus</i>	NULL	/	/	/	3961	/
	200	-0.38 (0.09)***	/	-0.53 (0.07)***	3579	Av. lum. + Inten. agri. + Exten. agri. + Forests + Roads + Temp.
	500	-0.37 (0.09)***	/	-0.44 (0.08)***	3573	
	700	-0.50 (0.10)***	/	-0.59 (0.08)***	3577	
	1000	-0.52 (0.10)***	/	-0.63 (0.08)***	3579	

The explanatory variables kept in the final model were significant in at least one of the 4 landscape scales considered.

Bold values represent the smallest model's AIC obtained for each species and indicate the landscape scale at which the model described best species response

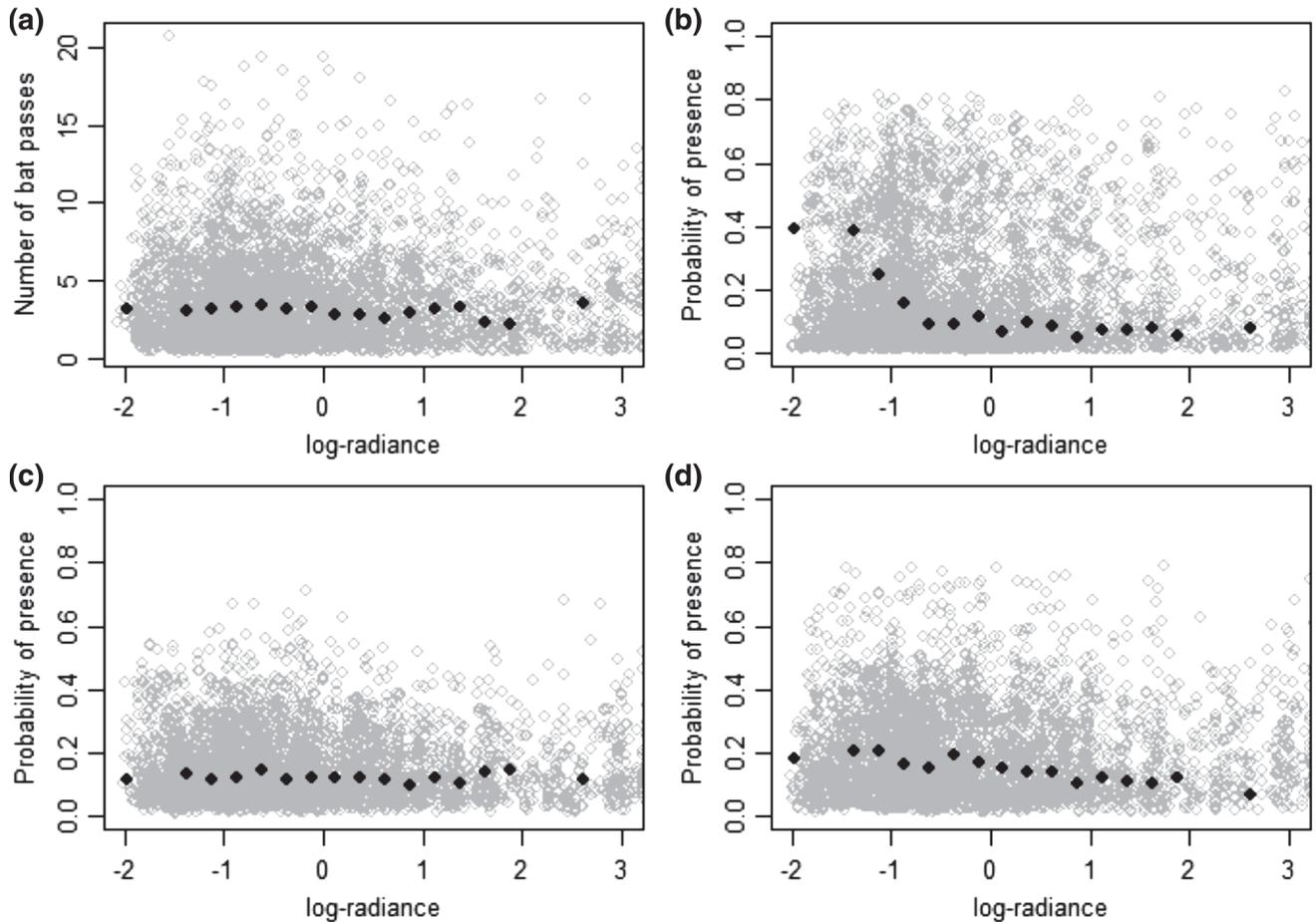


Fig. 4 Mean number of bat pass of *P. pipistrellus* (a), and mean probability of presence of *P. kuhlii*; *N. leisleri*, and *E. serotinus* (b, c, d respectively) per bin of 0.25 log-radiance, within a 200 m landscape scale for *P. pipistrellus* and *N.*

leisleri, a 500 m landscape scale for *P. kuhlii* and a 1000 m landscape scale for *E. serotinus*. The models ran at these landscape scales best predicted species activity and probability of presence (i.e., Table 2).

rural and peri-urban areas along low-traffic roads (for safety reasons). This variation in species responses to an intermediate level of impervious surface has also been observed for a wide range of taxa such as invertebrates, reptiles, amphibians and non-flying mammals (McKinney 2008). It would be interesting to reproduce this analysis in areas with a high level of impervious surface to see if similar patterns of response remain.

Nevertheless, although dense urban cores were under-sampled in the program, the proportion of each land cover as well as the average radiance around transects were representative of land-use in mainland France (Table 1). In this context, our results suggest that only considering the proportion of impervious surface as a proxy for urbanization may lead to underestimated impacts on biodiversity because light

pollution affects substantial parts of ecosystems surrounding urban areas (Kyba et al. 2011; Kyba and Hölker 2013; Gaston et al. 2015).

Unlike light-sensitive bats which are known to avoid illuminated areas (Stone et al. 2009, 2012), the 4 species in this study have often been recorded foraging under streetlights (Rydell 1992; Lacoëuilhe et al. 2014; Azam et al. 2015). At a local scale, they select 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 (Eisenbeis 2006; Perkin et al. 2014). Surprisingly, our results showed that these so-called “light-attracted” species only presented negative or neutral response to ALAN at a landscape scale. This suggests that even if a streetlight can present foraging advantages for some species of

bats locally, landscape-scale level of ALAN generates a landscape “filter” that negatively influences the occurrence and activity of bats in a given place.

This may be explained by the fact that ALAN does not only influence species foraging behavior, but also reproduction and commuting behaviors (Boldogh et al. 2007; Hale et al. 2015). First, artificial illumination of maternity roosts has major impacts on the fitness of juveniles and reproductive females by desynchronizing the timing of bat nightly emergence with insects’ peak of abundance (Jones and Rydell 1994; Downs et al. 2003; Boldogh et al. 2007). Landscape scale level of ALAN may hence exert an important pressure on the reproductive success of maternity colonies and decrease the availability of suitable roosts. Second, ALAN has been shown to decrease landscape connectivity by altering movements and gap-crossing behaviors of *P. pipistrellus* individuals in an urban matrix (Hale et al. 2015). Although bats are highly mobile and may be able to take alternative dark routes in the landscape, such effects may generate increased costs in flight time and in stress with important implications for individuals’ fitness especially during reproduction (Stone et al. 2009). So, it appears that, regardless of species foraging behavior, landscape-scale level of ALAN may significantly impact local population dynamics (Gaston and Bennie 2014). This hypothesis, consistent with Mathews et al. 2015, has important conservation implications as we can expect an even stronger impact of landscape-scale level of ALAN on light-sensitive species which are particularly negatively affected by habitat loss and fragmentation (Safi and Kerth 2004; Frey-Ehrenbold et al. 2013).

The massive insect mortality caused by ALAN (Eisenbeis 2006) is likely to have a negative effect on bats (Van Langevelde et al. 2011). Common macro-moths have experienced major declines in the UK in recent decades (Conrad et al. 2006), and it has been hypothesized that urban areas and their associated sky glow may act as long-term ecological sinks, depleting the surrounding landscapes of moth species (Bates et al. 2014). Crashes in insect populations in and around illuminated areas could explain landscape-scale negative effects of ALAN on bats.

Nevertheless, the effect of ALAN was weaker than the effect of intensive agriculture which was significantly negative for the 4 species at the 4 landscapes

scales considered. Agricultural intensification has been associated to dramatic declines in biodiversity because of the habitat loss; the clearance in structural connectivity elements such as hedgerows and the massive use of agrochemicals it generates (Donald et al. 2001; Wickramasinghe et al. 2004; Jennings and Pocock 2009). Bats are highly dependent on structural linear elements for commuting between roosting and foraging sites in agricultural landscapes (Downs and Racey 2006; Frey-Ehrenbold 2013; Vanderveelde et al. 2014). Furthermore, for a given microhabitat bat activity was significantly lower in conventional farms compared to organic farms, suggesting the important adverse effect of agrochemicals on prey density (Wickramasinghe et al. 2003). As nocturnal insectivorous species, bats’ response to land-use is likely to reflect the productivity of the impacted insect community (Jones et al. 2009). Therefore, the concomitant landscape-scale negative effects of intensive agriculture and ALAN may reflect a large scale depletion of prey resource in human-altered landscapes.

For the last century, worldwide human population has experienced a major increase in the number of urban dwellers (Grimm et al. 2008; United Nations 2014). This has led to a massive expansion of cities and human infrastructures with important consequences on biodiversity and ecosystems functions within urban areas but also in peripheral natural and semi-natural habitats (McKinney 2008; McDonald et al. 2008). In this context, our results show the importance of integrating light pollution issues in sustainable urban-planning schemes to allow the persistence of biodiversity in anthropogenic landscapes (Kyba et al. 2011; Gaston et al. 2015). Such schemes should be scheduled in urban and peri-urban areas to illuminate only where and when it is needed with a particular emphasis on the enhancement of dark shelters in human-dominated landscapes (Gaston et al. 2012). These recommendations are of particular relevance considering that we are currently at an important crossroad in lighting management, as lighting equipment reaches its end-of-life in developed countries and is expanding in developing countries. Both trends occur concomitantly with the emergence of energy-efficient lamps such as Light Emitting Diode (Hölker et al. 2010). Such technologies offer many opportunities to limit light pollution by controlling streetlamp parameters (light spectrum, intensity and directionality) at a local scale (Kyba et al. 2014).

However, the enhancement of the luminous efficiency of LED technologies and subsequent energy saving may come with a “rebound effect” because their cost-effectiveness may lead to an increased use of outdoor lighting in previously unlit areas (Kyba et al. 2014). In this context, our results highlight that careful outdoor lighting planning at large spatial scales is crucial to conciliate biodiversity and urban development, and avoid increasing light pollution phenomena.

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Online Appendices

Table S1. Detailed information on the French national bat-monitoring program (<http://vigienature.mnhn.fr/>), coordinated by the National Museum of Natural History (MNHN).

Aim of the program	Monitoring the temporal trends of bat populations at a national scale	
Sampling protocol		
<i>Scope</i>	10 km around surveyors' home.	
<i>Circuit length</i>	30 km	
<i>Number of transect per circuit</i>	10	
<i>Transect length</i>	2 km separated of at least 1 km	
<i>Period of sampling</i>	from the 15 th of June to the 31 th of July	
<i>Weather conditions</i>	no rain, low wind speed (< 7 m/s), temperature > 12°C	
<i>Survey start</i>	30 minutes after sunset	
Bat recording characteristics		
<i>Acoustic detectors</i>	Tranquility Transect Bat detector&D240x	
<i>Intercalibration of detectors</i>	At the MNHN	
Acoustic settings	<i>Tranquility Transect</i>	<i>D240x</i>
<i>Suppliers</i>	Courtpan Design Ltd, UK	Pettersson Elektronik
<i>High pass filter</i>	5 kHz	18 kHz
<i>Frequency</i>	96 000 sample/sec	96 000 sample/sec
<i>Record length (sec)</i>	0.32	0.1
<i>Post-recording treatment</i>	/	Elimination of acoustic sequences spaced of less than 3.2 sec.
<i>Time expansion</i>	X10	X10
<i>Recording device</i>	Zoom H2 digital recorder (Samson technologies, USA)	
<i>File storage format</i>	WAV	
Bat identification		
<i>Software</i>	Syrinx 2.6	
<i>Procedure</i>	<ul style="list-style-type: none"> - Training: 2-day training course+ online self-training courses - Bat first identification: by volunteers - Bat identification validation: by MNHN 	
<i>Taxon identification level</i>	Species level for all species except for <i>Myotis sp.</i> + Analysis of <i>P. kuhlii</i> number of bat pass on 270 transects showed that <i>Pipistrellus kuhlii</i> response variable may include less than 8 % <i>Pipistrellus nathusius</i> , as these two species overlap in their acoustic signatures.	

Table S2. Effects of the bat detector (either D240X of Tranquility Transect) and the age of microphones (Age) on the duration of bat pass detected of a sample of direct acoustic recordings of the FBMP. The table shows the averaged partial regression coefficient and p-value from GLMMs. Bold police indicates P-value < 0.05.

	<i>P. pipistrellus</i> <i>N=5070</i>	<i>P. kuhli</i> <i>N=549</i>	<i>E. serotinus</i> <i>N=487</i>	<i>N. Leisleri</i> <i>N=256</i>
Bat detector	<i>P=0.03 ; D240x>TT</i>	<i>P=0.74</i>	<i>P=0.16</i>	<i>P=0.95</i>
Age	<i>P=0.11</i>	<i>P=0.06</i>	<i>P=0.95</i>	<i>P=0.43</i>
Bat detector : Age	<i>P=0.26</i>	<i>P=0.76</i>	<i>P=0.84</i>	<i>P=0.27</i>

Table S3. Correlation coefficients of the 7 landscape variables included in the analysis (i.e. the average luminance, the proportions of impervious surface, intensive agriculture, extensive agriculture, forests, the total length of primary roads and streams (m)), at the 1000 m landscape-scale which showed the strongest the correlation coefficients between landscape variables.

Landscape Variables	Correlation coefficients					
	<i>Imper. surf.</i>	<i>Inten. agri.</i>	<i>Exten. agri.</i>	<i>Forests</i>	<i>Roads</i>	<i>Streams</i>
<i>Av. luminance</i>	0.85	-0.10	-0.14	-0.07	0.13	0.02
<i>Imper.surf.</i>	/	-0.12	-0.16	-0.06	0.14	0.04
<i>Inten. agri.</i>	/	/	-0.32	-0.46	0.04	-0.30
<i>Exten. agri.</i>	/	/	/	-0.25	-0.007	0.09
<i>Forest</i>	/	/	/	/	-0.02	-0.007
<i>Roads</i>	/	/	/	/	/	-0.009

Table S4. Averaged partial regression coefficient and associated standard errors from multi-model averaging of the 9 fixed effects included in the analysis (i.e. the average luminance, the proportions of impervious surface, intensive agriculture, extensive agriculture, forests, the total length of primary roads and streams (m), and the date and temperature) for the 4 species and at 4 landscape scales considered. Bold police indicates that the estimates were significantly different from 0 (P-value < 0.05).

Species	Scale	Av. luminance	Imper. surf.	Inten. agri.	Exten. agri.	Forests	Roads	Streams	Date	T°C
<i>P. pipistrellus</i>	200	-0.08 (0.02)	0.05 (0.01)	-0.15 (0.02)	-0.02 (0.01)	0.09 (0.01)	-0.01 (0.01)	0.03 (0.00)	0.10 (0.01)	0.06 (0.01)
	500	-0.01 (0.02)	0.03 (0.01)	-0.10 (0.02)	0.01 (0.01)	0.12 (0.02)	-0.03 (0.01)	0.05 (0.00)	0.10 (0.01)	0.06 (0.01)
	700	-0.02 (0.02)	-0.001 (0.01)	-0.11(0.02)	0.01 (0.01)	0.11 (0.01)	-0.01 (0.01)	0.05 (0.01)	0.10 (0.01)	0.06 (0.01)
	1000	-0.01 (0.01)	-0.01 (0.02)	-0.11 (0.02)	0.02 (0.02)	0.11 (0.01)	-0.009 (0.01)	0.06 (0.01)	0.10 (0.01)	0.06 (0.01)
<i>P. kuhlii</i>	200	-0.22 (0.10)	-0.04 (0.02)	-0.41 (0.09)	0.10 (0.06)	-0.16 (0.06)	0.06 (0.04)	-0.02 (0.05)	0.02 (0.07)	0.11 (0.06)
	500	-0.25 (0.10)	-0.09 (0.06)	-0.46 (0.10)	0.14 (0.06)	-0.14 (0.07)	0.07 (0.05)	0.02 (0.05)	0.02 (0.07)	0.11 (0.06)
	700	-0.26 (0.05)	-0.15 (0.07)	-0.42 (0.04)	0.06 (0.02)	-0.14 (0.02)	0.02 (0.02)	0.04 (0.02)	0.02 (0.02)	0.07 (0.02)
	1000	-0.33 (0.10)	-0.24 (0.09)	-0.64 (0.10)	0.12 (0.07)	-0.25 (0.07)	0.01 (0.05)	0.08 (0.06)	0.04 (0.06)	0.13 (0.06)
<i>E. serotinus</i>	200	-0.40 (0.09)	0.01 (0.07)	-0.58 (0.07)	-0.19 (0.06)	0.08 (0.05)	0.07 (0.04)	-0.08 (0.04)	0.01 (0.06)	0.19 (0.06)
	500	-0.35 (0.10)	-0.01 (0.04)	-0.43 (0.08)	-0.07 (0.08)	0.23 (0.06)	0.10 (0.05)	-0.02 (0.05)	0.01 (0.05)	0.18 (0.06)
	700	-0.42 (0.09)	-0.08 (0.06)	-0.43 (0.06)	-0.13 (0.05)	0.04 (0.04)	0.01 (0.03)	-0.02 (0.03)	0.02 (0.04)	0.13 (0.05)
	1000	-0.52 (0.10)	-0.13 (0.07)	-0.65 (0.08)	-0.21 (0.07)	0.05 (0.07)	0.03 (0.05)	-0.02 (0.05)	0.02 (0.05)	0.19 (0.07)
<i>N. leisleri</i>	200	-0.06 (0.06)	0.15 (0.06)	-0.22 (0.08)	-0.11 (0.07)	-0.03 (0.08)	-0.03 (0.05)	0.20 (0.05)	0.06 (0.06)	0.28 (0.06)
	500	-0.01 (0.08)	0.04 (0.04)	-0.17 (0.07)	-0.15 (0.07)	0.07 (0.07)	-0.01 (0.04)	0.23 (0.05)	0.06 (0.06)	0.28 (0.06)
	700	-0.05 (0.07)	0.07 (0.06)	-0.12 (0.06)	-0.19 (0.07)	-0.02 (0.06)	0.01 (0.05)	0.17 (0.03)	0.05 (0.05)	0.21 (0.05)
	1000	-0.06 (0.08)	0.08 (0.07)	-0.16 (0.08)	-0.25 (0.08)	-0.05 (0.08)	0.05 (0.05)	0.23 (0.06)	0.05 (0.06)	0.27 (0.06)

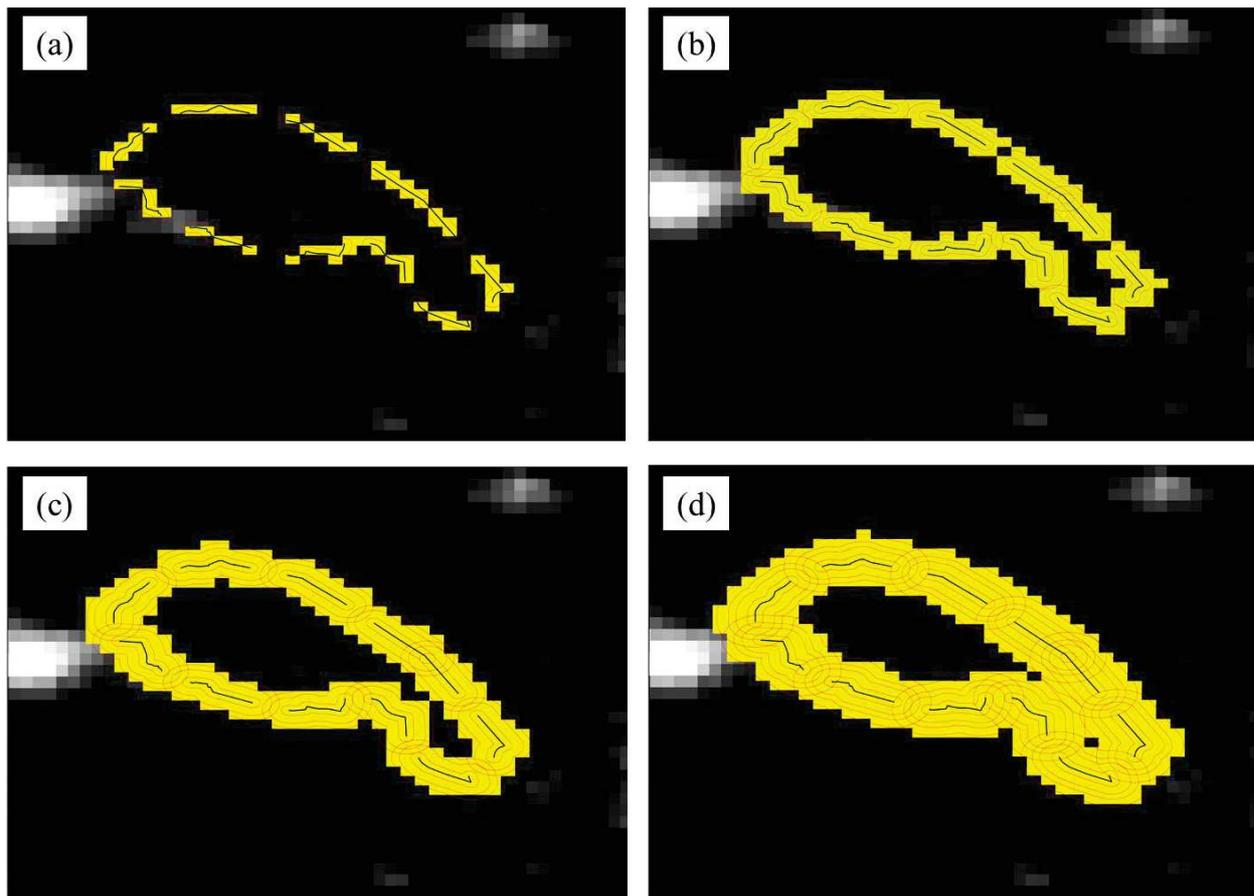


Figure S1. Demonstration of the procedure done to calculate average radiance within the buffers of (a) 200 m, (b) 500 m, (c) 700 m and (d) 1000 m width from the VIIRS Nighttime Light raster used to. The average radiance was computed by the tool “zonal statistics as Table” from the package “Spatial Analyst” of ArcGIS 10.2 which proceed by creating a raster (yellow) from the polygon shapefile input (red) before applying an internal resampling so that input raster resolution match with the resolution of the VIIRS Nighttime Light raster.

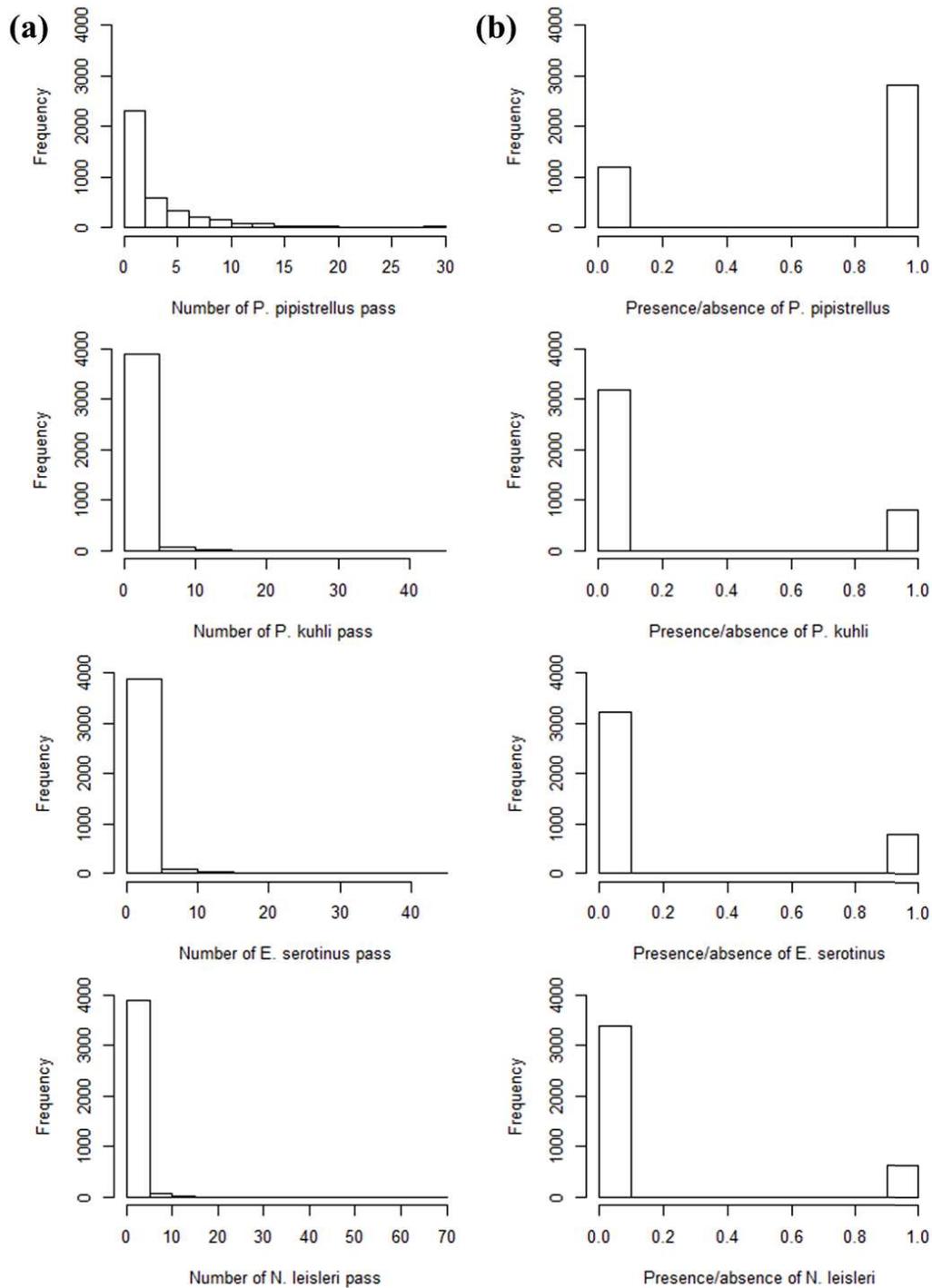


Figure S2. Distribution of the response variable of *P. pipistrellus*, *P. kuhli*, *E. serotinus* and *N. leisleri* in number of bat pass per transect at the left hand side of the figure (a), and in presence/absence at the right hand side of the figure (b). We chose to follow a poisson distribution for *P. pipistrellus*, and a binomial distribution for *P. kuhli*, *E. serotinus* and *N. leisleri* for statistical analyses.

Discussion & Perspectives

This paper revealed the landscape-scale negative effects of nighttime artificial lighting on the activity and probability of occurrence of 4 common species of bats. It also showed that light pollution had a stronger negative effect than the proportion of impervious surface. This suggests that the impacts of urbanization on biodiversity may be underestimated by not taking into account light pollution, which is emitted by urban areas and propagates way beyond its sources of emissions (Kyba & Hölker 2013). Yet, most macroecological studies so far used the proportion of impervious surface as a proxy for urbanization process (McKinney 2002; Penone et al. 2013; Deguines et al. 2016). Thus, this paper suggests that nighttime artificial lighting data should be implemented in such studies as this data encompasses both the effects of impervious surfaces and of light pollution. In this context, the recent development of global maps of artificial night sky brightness thanks to new high resolution satellite data (Falchi et al. 2016) offers great opportunities to integrate light pollution issues in the large-scale monitoring of biodiversity responses to global changes.

It is also important to note that this first chapter only investigated the effects of land-use and light pollution on the activity and occurrence of the 4 most common species of bats in France, without integrating the temporal trends of populations. It appears that these common species present important declines in France (Figure 7; Kerbiriou et al. 2015) and in Great Britain (Roche et al. 2011; Barlow et al. 2015). In this context, it would be of major interest to quantify the extent of effect of land-use and of light pollution on these observed declines. Such analyses could allow determining if species are declining faster in illuminated areas compared to dark ones, but also quantifying the effects of change in outdoor lighting strategies (e.g. decline or increase in brightness or modernization of infrastructure; Bennie et

al. 2014a) on bat temporal trends, using historical and contemporary satellite data of nighttime lights.

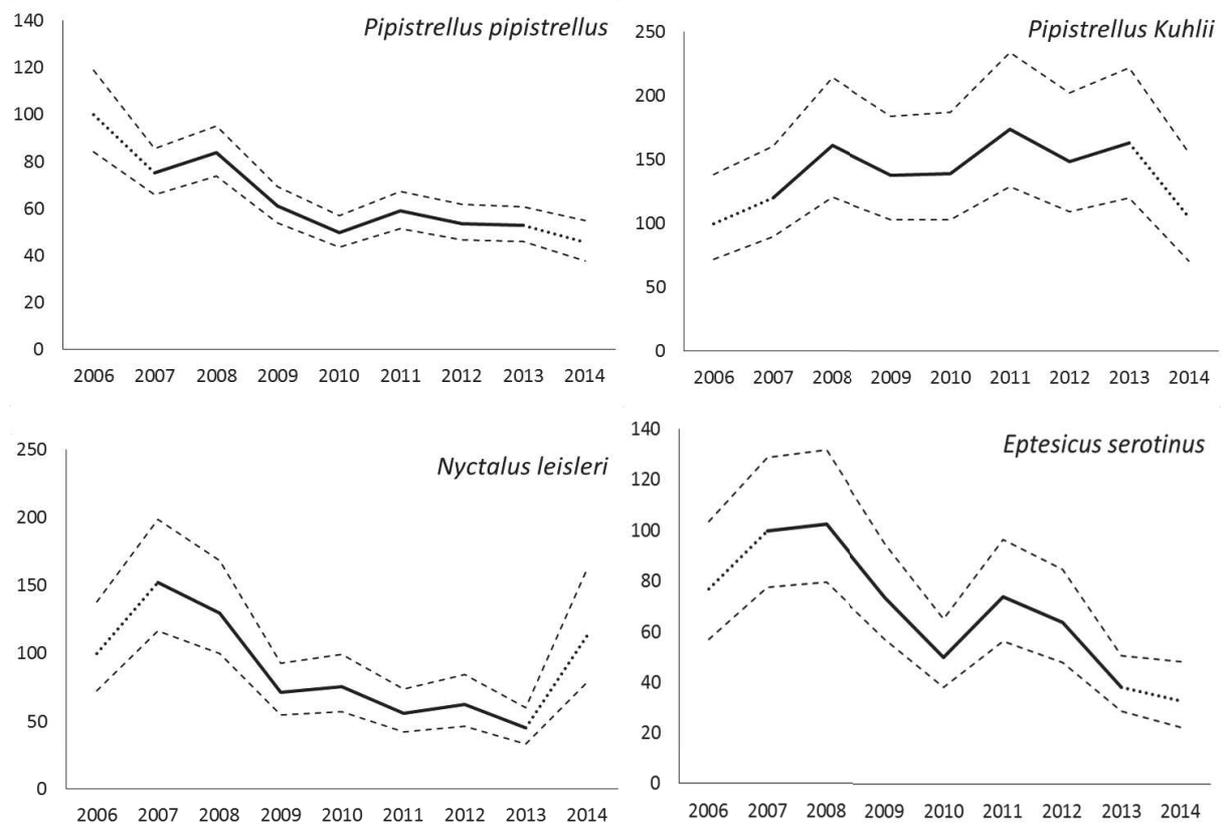


Figure 7. Extracted from Kerbiriou et al. (2015) presenting the national population trends of *P. pipistrellus* and *P. kuhlii*, *N. leisleri*, and *E. serotinus* from 2006 to 2014 in France (Data from the French National Bat Monitoring Program “Vigie-Chiro”, <http://vigienature.mnhn.fr/page/vigie-chiro>).

In this paper, we hypothesized 3 underlying ecological mechanisms that may explain the negative effect of landscape-scale level of nighttime artificial lighting on bats species that have often been reported to forage under streetlights. First, illuminated landscapes may be subjected to a large depletion of insect biomass because artificial lighting induces massive mortality on insect populations (Eisenbeis 2006), disrupts moth reproductive behaviors (van Geffen et al. 2015b) and impedes their dispersal movements (Degen et al. 2016). This is of particular concern as a national scale study in Great Britain showed that common species of moths have experienced rapid declines in the last 30 years (Conrad et al. 2006). Thus, it would be interesting to study the landscape-scale effects of light pollution on nocturnal insects

species or biomass in order to assess whether the patterns of response detected are similar to the ones we observed for bats. Second, we hypothesized that the landscape-scale negative effect of light pollution on bat activity and occurrence may be linked to the “barrier” effect artificial lighting can induce on bat movements in a landscape (Kuijper et al. 2008a; Stone et al. 2012; Hale et al. 2015). This negative effect on landscape connectivity may increase daily energetic costs during reproduction by increasing the distance between maternity roosts and suitable foraging sites (Stone et al. 2009), and may also limit the dispersal abilities of individuals during swarming periods in autumn. These aspects will be discussed in Chapter 3.

Finally, we hypothesized that the patterns of response characterized in this paper may be partly due to the negative effect outdoor lighting may have on the roost selection patterns of reproductive colonies. The gregarious behavior of female bats during reproduction implies the selection of roosting sites that are located within a landscape with high quality foraging patches in order to avoid competition between conspecifics (Arthur et al. 2014). In this context, the amount of nighttime artificial lighting in a given area may reduce the size and accessibility of suitable foraging sites, generate additional energetic costs associated to transit, and hence decrease the suitability of the area for maternity roost settlement. To investigate this question, I co-supervised the Master Project of Laurie Burette with Isabelle Le Viol and Christian Kerbiriou, as well as Laurent Arthur and Michèle Lemaire of the Museum of Natural History of Bourges (Centre Region, France). The aim of this project was to analyze the effects of outdoor lighting on maternity roost selection and on the timing of emergence of female bats (Burette 2014). To answer these 2 questions, we used the position of known maternity roosts compiled by the Museum of Natural History of Bourges in the department of the Cher (over 1200 maternity roosts belonging to 13 species, Figure 8), and we monitored the timing of emergence of females from a subset of these maternities. At a local scale, Laurie Burette found that the illumination of the entrance of maternity roosts of *E. serotinus* induced

a delay in the emergence of females at dusk. This is consistent with the literature and suggest that immediate darkness around maternity roosts is of major importance to ensure the reproductive success of bat colonies (Boldogh et al. 2007; Russo et al. 2007). At a regional scale, we initiated an analysis on the effect of streetlight density on the roost selection patterns of 4 species of bats (*R. hipposideros*, *Barbastella barbastellus*, *E. serotinus* and *P. pipistrellus*) with Species Distribution Models (SDM), using the position of maternity roosts as a response variable (See Appendix 1 for details on the methods; Fonderflick et al. 2015). This analysis is not finalized yet, but it will allow i) characterizing how artificial lighting can influence the availability of suitable roosting areas, and ii) building Habitat Suitability Maps that can inform sustainable land-use planning strategies (Bellamy & Altringham 2015; Fonderflick et al. 2015).

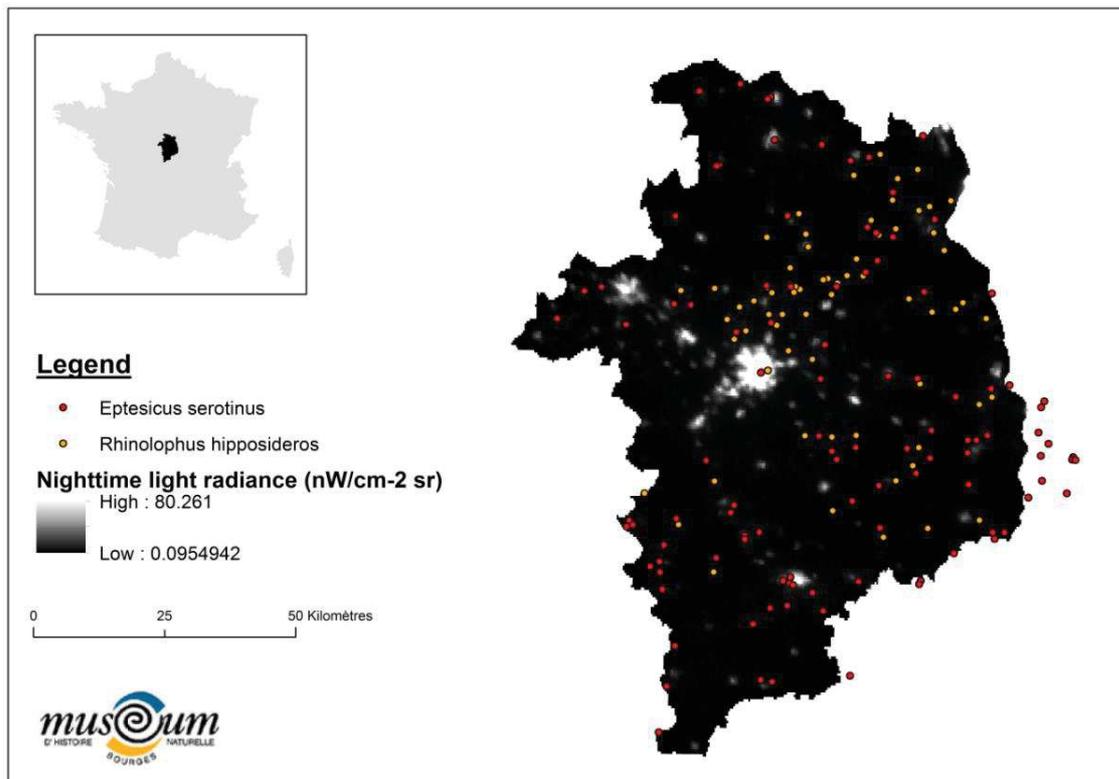


Figure 8. Nighttime light radiance over the Cher, France (extracted from European VIIRS raster) and distribution of the known maternity roosts of *E. serotinus* (red, n = 106) and *R. hipposideros* (orange, n = 69) in the Cher, France.

CHAPTER 2:

Limiting the temporal extent of artificial lighting to reduce the negative impacts of outdoor lighting on bat activity

Based on the publication :

Azam C, Kerbiriou C, Vernet A, Julien JF, 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**:4333–4341.

Introduction

The previous chapter revealed the landscape-scale negative effect of nighttime artificial lighting on bat activity and occurrence. We hypothesized that such effect may be due to a decrease i) in insect biomass in illuminated landscapes; ii) in landscape connectivity inducing higher energetic costs and limited dispersal abilities; iii) in the suitability of illuminated landscapes for maternity roost settlement and reproductive success. This highlights the importance of integrating outdoor lighting management in land-use planning in order to restore darkness in human-inhabited landscapes.

In this context, limiting the temporal extent of outdoor lighting, by turning-off streetlights during time periods when most humans are asleep, is quite easy to implement and appears to be an interesting option to restore darkness in a landscape for at least a part of the night. Many local administrations from rural areas over Europe (1/3 in the UK, CPRE 2014) have developed part-night lighting schemes by turning-off streetlights from midnight (+/- 1 hours) to early morning (05-06 AM). These schemes have mostly been set up to save energy and money (CPRE 2014), as outdoor lighting represents 41 % of the energy consumption of local administrations and 37 % of localities electricity bills in France (ADEME 2005).

However, the effectiveness of these schemes in limiting the adverse impacts of light pollution on biodiversity is largely unknown. It has been suggested that they are unlikely to encompass the nightly rhythm of nocturnal species which are mostly active right after dusk (Gaston et al. 2012). For example, most insect biomass is available at dusk (Figure 9; Jetz et al. 2003), and the peak of activity of microlepidoptera occurs during the first 2 hours after sunset (Knight et al. 1994). Unsurprisingly, nocturnal insectivores such as microchiropteran bats and nightjars appear to follow the same pattern of activity (Jones & Rydell 1994; Jetz et al. 2003). In this context, part-night lighting schemes may not effectively limit the adverse impacts of artificial

lighting on nocturnal biodiversity as it is unlikely to encompass the peak of activity of most species.

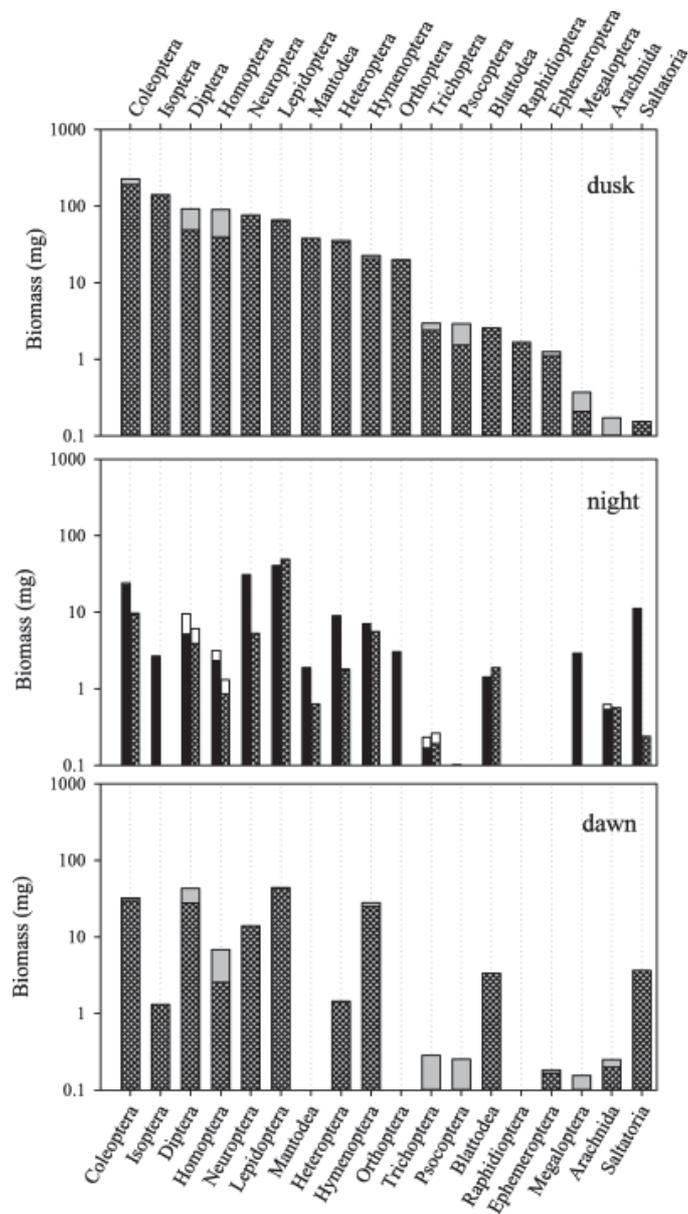


Figure 9. Extracted from Jetz et al. (2003) describing the biomass of insect orders sampled with car traps at different times of the night. Hatched parts of bars indicate biomass of insects >3 mm only. Night: left bar first half, right bar second half of the night.

However, bat maternity roosts have relatively large home ranges, and females can go several kilometers away from their roost to find suitable foraging sites (e.g. 15 km for *Myotis emarginatus* and *R. ferrumequinum*; Fonderflick et al. 2015), suggesting that they can be out of their roosts for an important part of the night. Furthermore, lactating females, which are

under high energetic constraints, are active most part of the night during reproduction, with several entries and exits from their roosts through the night to feed their offsprings (Henry et al. 2002). Thus, part-night lighting schemes may have positive effects on bat foraging and transit activities in summer, by increasing landscape connectivity and give access to additional foraging resources for a part of the night.

In this context, we intended to determine what was the effect of part-night lighting on the activity of microchiropteran bats, in comparison to standard full-night lighting schemes and to dark control. We set up a paired *in situ* experiment in the Natural Park of the French Gâtinais which is a rural area located 60 km south from Paris. This protected areas has been promoting part-night lighting schemes to local representatives for several years. Following this campaign, half of the localities have started turning-off public streetlights from approximately 23-00h to 05-06h AM for at least 2 years (Figure 10).

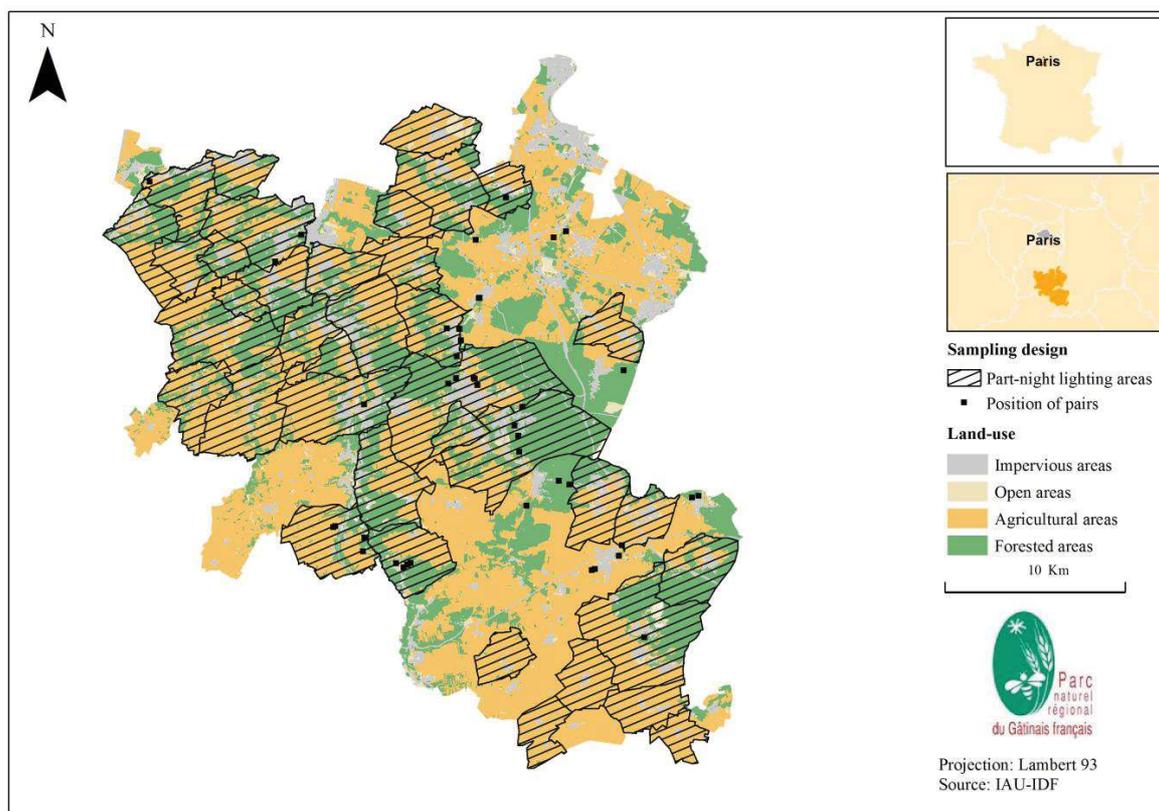


Figure 10. Map extracted from Azam et al. (2015) presenting the 36 pairs of study sites with respect to the local administrations practicing part-night lighting and the regional land uses.

Is part-night lighting an effective measure to limit the impacts of artificial lighting on bats?

CLÉMENTINE AZAM¹, CHRISTIAN KERBIRIOU¹, ARTHUR VERNET², JEAN-FRANÇOIS JULIEN¹, YVES BAS¹, LAURA PLICHARD², JULIE MARATRAT² and ISABELLE LE VIOL¹

¹National Museum of Natural History, 55 rue Buffon, Center for Ecology and Conservation Science, UMR7204-MNHN-CNRS-UPMC, 75005 Paris, France, ²Parc Naturel Régional du Gâtinais Français, Maison du Parc 20 boulevard du Maréchal Lyautey, 91490 Milly-la-Forêt, France

Abstract

As light pollution is currently considered to be a major threat to biodiversity, different lighting management options are being explored to mitigate the impact of artificial lighting on wildlife. Although part-night lighting schemes have been adopted by many local authorities across Europe to reduce the carbon footprint and save energy, their effects on biodiversity are unknown. Through a paired, *in situ* experiment, we compared the activity levels of 8 bat species under unlit, part-night, and full-night lighting treatments in a rural area located 60 km south of Paris, France. We selected 36 study locations composed of 1 lit site and a paired unlit control site; 24 of these sites were located in areas subject to part-night lighting schemes, and 12 sites were in areas under standard, full-night lighting. There was significantly more activity on part-night lighting sites compared to full-night lighting sites for the late-emerging, light-sensitive *Plecotus* spp., and a similar pattern was observable for *Myotis* spp., although not significant. In contrast, part-night lighting did not influence the activity of early emerging bat species around streetlights, except for *Pipistrellus pipistrellus* for which there was significantly less activity on part-night lighting sites than on full-night lighting sites. Overall, no significant difference in activity between part- and full-night lighting sites were observed in 5 of the 8 species studied, suggesting that current part-night lighting schemes fail to encompass the range of activity of most bat species. We recommend that such schemes start earlier at night to effectively mitigate the adverse effects of artificial lighting on light-sensitive species, particularly along ecological corridors that are especially important to the persistence of biodiversity in urban landscapes.

Keywords: bats, Chiroptera, land-use planning, outdoor lighting regulations, part-night lighting, urbanization

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Introduction

Given the current degree of urbanization (United Nations, 2014) and its severe impacts on biodiversity (McKinney, 2006; McDonald *et al.*, 2008), characterizing its effects on biological communities is of major importance (Luniak, 2004; Jung & Kalko, 2010; Hale *et al.*, 2012; Penone *et al.*, 2013; Bates *et al.*, 2014).

Artificial lighting is intrinsically associated with urban sprawl; it has been deployed at a massive scale over the last century and continues to spread at an annual rate of increase of 6% worldwide (Cinzano *et al.*, 2001; Hölker *et al.*, 2010a). As a result, major concerns have been raised about the hidden impacts of artificial lighting and the associated light pollution on biodiversity and ecosystem functioning (Rich & Longcore, 2006; Navara & Nelson, 2007; Hölker *et al.*, 2010b).

Ecological light pollution alters natural light regimes (Longcore & Rich, 2004; Hölker *et al.*, 2010b), and it

affects the rhythms of activity of populations of both diurnal and nocturnal species with important implications for individual fitness, sexual selection, and reproductive success (Miller, 2006; Boldogh *et al.*, 2007; Kempenaers *et al.*, 2010; Titulaer *et al.*, 2012; Le Tallec *et al.*, 2013; Nordt & Klenke, 2013). Furthermore, the responses of species to artificial lighting are driven by attraction/repulsion behaviors, so the movements and distribution of species can be altered at multiple spatial scales (Longcore & Rich, 2004). Taken together, the effects of artificial lighting can dramatically affect biological communities (Davies *et al.*, 2012, 2013; Gaston *et al.*, 2013, 2014).

In this context, designing outdoor lighting regulations that save energy and reduce CO₂ emissions while limiting the ecological impacts of artificial lighting is a major challenge in land-use planning (Hölker *et al.*, 2010a). Different lighting parameters, such as street-lamp spectrum, intensity, directionality, and duration of lighting, can be managed to limit the negative effects of artificial lighting on biodiversity (Gaston *et al.*, 2012;

Correspondence: Clémentine Azam, tel./fax +33 (0)1 40 79 38 31, e-mail: cazam@mnhn.fr

Kyba *et al.*, 2014). In an attempt at mitigation, many local authorities in Europe have started switching off public streetlights in the middle of the night, primarily to reduce local electricity costs and to save energy (Ben- nie *et al.*, 2014).

It has been suggested that this measure, so-called part-night lighting, is unlikely to limit the impacts of artificial lighting on biodiversity because it does not coincide with the activity peaks of most nocturnal organisms, which occur at dusk when public demand for outdoor lighting is very high (Gaston *et al.*, 2012). Consistent with this hypothesis, subjecting the light-sensitive bat *R. ferrumequinum* to simulated part-night lighting scenarios revealed that such schemes are unlikely to be compatible with its peak activity (Day *et al.*, 2015). However, no study has tested the effect of this measure at the community level by simultaneously comparing the responses of multiple species to part-night lighting schemes.

As they are nocturnal and directly exposed to light pollution, microchiropteran bats are good candidates to test the effects of part-night lighting schemes on biodiversity. Increasingly threatened worldwide (Mickleburgh *et al.*, 2002), bats are considered to be indicators of the response of biodiversity to anthropogenic pressure (Jones *et al.*, 2009). Microchiropterans are long-lived insectivorous species, and it has been suggested that their population trends reflect those of lower trophic level species (Jones *et al.*, 2009; Stahlschmidt & Brühl, 2012). Furthermore, several studies have pointed to their value in terms of providing ecosystem services, such as pest control (Cleveland *et al.*, 2006).

Artificial lighting can affect bats in different ways, both in time and space. For many species, including bats, the natural light regime is a cue that synchronizes their window of activity with their environment (Gaston *et al.*, 2013, 2014). The artificial illumination of maternity roosts can delay the emergence of female bats (Downs *et al.*, 2003; Boldogh *et al.*, 2007), which has important fitness costs for reproductive females as they miss the peak abundance of insects at dusk (Rydell, 1992; Jones & Rydell, 1994).

Artificial lighting can also modify resource availability and change species foraging patterns. Slow-flying species adapted to prey on insects in cluttered vegetation, such as *Rhinolophus* spp., *Myotis* spp., and *Plecotus* spp., appear to completely avoid illuminated areas (Rydell, 1992; Stone *et al.*, 2009, 2012; Kuijper *et al.*, 2008) due to increased predation risk from owls and other raptors (Jones & Rydell, 1994; Rydell *et al.*, 1996). In contrast, fast-flying species adapted to hunt insects in the open air, such as *Pipistrellus pipistrellus*, appear to benefit from new and predictable foraging opportunities provided by streetlights (Rydell, 1992; Blake *et al.*, 1994),

which attract a large portion of the surrounding insect biomass (Eisenbeis, 2006; Perkin *et al.*, 2014). However, even the movements and gap-crossing behaviors of light-attracted species in urban landscapes can be altered by artificial lighting (Hale *et al.*, 2015). Therefore, these differences in the response of species to artificial lighting likely induce important changes in the structure of bat communities (Arlettaz *et al.*, 2000; Polak *et al.*, 2011) and raise concerns about ecosystem function.

In this study, we intended to determine whether current part-night lighting schemes effectively limit the impacts of artificial lighting on bats in an inhabited rural region of France. We compared the level of activity of eight species of bats as measured by ultrasound recordings under dark (unlit), part-night, and full-night lighting conditions. We expected to find no difference in activity between part- and full-night lighting treatments for fast-flying species, whose peak activity is known to occur at dusk to exploit the evening peak in insect abundance (Jones & Rydell, 1994; Rydell *et al.*, 1996). However, we expected a potentially positive response from slow-flying species, with more activity on part-night lighting sites than on full-night lighting sites as they are the most light-sensitive species, and they are known to be active later at night than fast-flying species (Jones & Rydell, 1994; Rydell *et al.*, 1996). Furthermore, slow-flying species may also take advantage of the insect biomass attracted by streetlights, once they are turned off.

Materials and methods

Study area

The field experiment was set up in a protected, 849 km² regional park established to promote the sustainable use of natural resources and ecosystems (IUCN Protected Area Category VI), which is located 60 km south of Paris, France. Arable lands represent 58 % of the area, and forests comprise 31 %. Currently, urban areas make up 8 % of the park and are mostly composed of small towns and villages (Fig. 1), but the entire region is subject to pressures from urbanization due to its vicinity to the capital. The park is comprised of 69 municipalities that average 12 km² in size, and 56 % have employed part-night lighting schemes for at least 2 years. These schemes are designed to turn off all public streetlights from midnight (± 1 h) to 5:00 hours, representing approximately 65 % of the duration of the night.

Sampling design

We compared bat activity levels under unlit, part-night, and full-night lighting treatments through a paired *in situ* experiment. We selected 36 study locations composed of 1 lit site and a paired, unlit control site ($n = 72$ sites); 24 pairs were located in administrations practicing part-night lighting

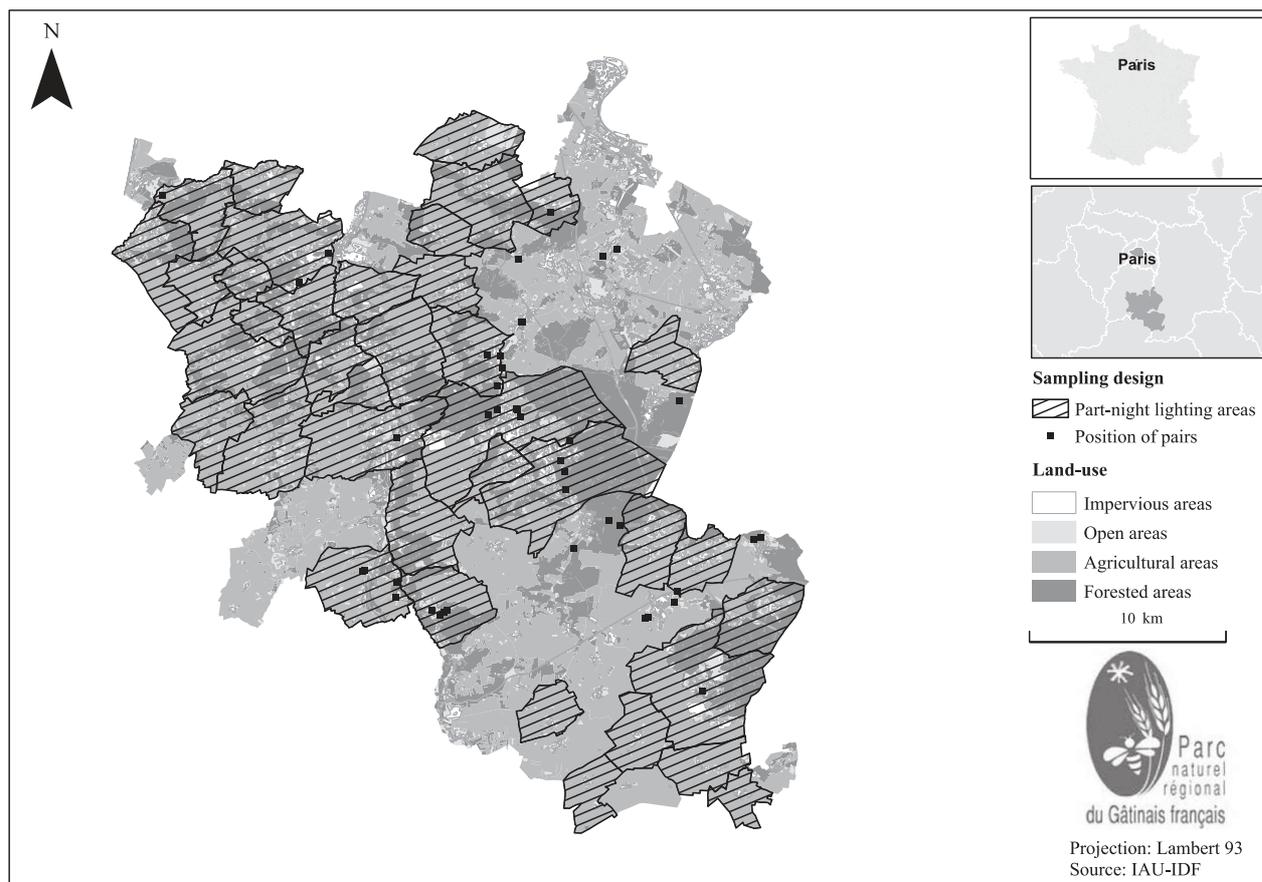


Fig. 1 Map of the 36 pairs of study sites with respect to the local administrations practicing part-night lighting and the regional land uses.

schemes, and 12 were located in municipalities with full-night lighting (Fig. 1). Lit sites were illuminated by 1 high-pressure sodium (HPS) vapor streetlamp (average intensity = 32 lux; range = 10–99 lux) and located away from the town cores to limit any correlation between light treatment and urbanization. Unlit sites were separated from their paired lit site by approximately 250 m, but pairs were located in similar habitats and set along the same types of bat commuting routes, such as forest edges and hedgerows (Walsh & Harris, 1996; Downs & Racey, 2006). The 2 sites of each pair were also located at similar distances from linear elements, such as roads and streams.

We ensured that light treatment was not correlated with the surrounding land uses, especially the proportion of impervious areas, in our study area. We created circular buffers with radii ranging from 50 to 2000 m around each sampled site ($n = 72$) using GIS (ARCGIS 10/ESRI; <http://www.esri.com/>) and calculated the proportion of forested, arable, impervious (urban and roads), and open (meadows and gardens) areas using a detailed regional geo-referenced land-use database with a resolution of 25 m (IAURIF, 2008). We then tested the correlation between light treatment and these land-use variables at 6 different spatial scales using a Kruskal–Wallis one-

way analysis of variance. We detected significant differences between the 3 light treatments at only small, from 50 to 250 m, spatial scales (Table S1), but these differences did not result in any multicollinearity problems (Variance Inflation Factor (VIF) < 3; Fox & Monette, 1992).

Bat monitoring

Fieldwork was carried out (i) from the first of May to the 28th of August, which corresponds to the seasonal peaks in the activities of the bat species as recommended by the French national bat-monitoring program 'Vigie-Chiro' (<http://vigienature.mnhn.fr/>); (ii) when weather conditions were favorable, that is, no rain, low wind speed ($< 7 \text{ m s}^{-1}$), and temperatures higher than 12 °C; (iii) between the third and the first quarter moon to limit the interaction between natural and artificial lighting (Saldaña-Vázquez & Munguía-Rosas, 2013).

Both sites of each pair (1 lit/1 unlit) were sampled on the same night from 30 min before sunset to 30 min after sunrise. Standardized echolocation calls were simultaneously recorded using 1 stationary SM2BAT (<http://www.wildlifeacoustics.com/>) detector per site, which allowed for the direct comparison of bat activity between the 2 sites of each pair. The

detectors automatically recorded all ultrasound (> 12 KHz) while maintaining the characteristics of the original signals. Ambient temperature was also recorded every 30 min for each pair with an EL-USB-1 temperature data logger (Lascar Electronics, Salisbury, UK).

We used the software SonoChiro© (Bas *et al.*, 2013) to automatically classify the echolocation calls to the most accurate taxonomic level possible. We then checked the software classification by screening all ambiguous calls with Syrinx software version 2.6 (Burt, 2006). Identification was possible to the species level in all but two genera, *Plecotus* spp. and *Myotis* spp., due to the very low occurrence of the individual species and uncertainties in the acoustic identification to the species level (Obrist *et al.*, 2004; Barataud, 2012). Note that we expected similar responses to the light treatments from the species in these two genera as they appear to have similar foraging behaviors (Arlettaz *et al.*, 2001). As it is impossible to distinguish individual bats from their echolocation calls, we calculated an index of relative bat activity for each sample site, which was defined as the mean number of bat passes per species. A bat pass is defined as the occurrence of a single or several bat calls during a 5-s interval (Millon *et al.*, 2015).

Statistical analysis

For each species, we created a general linear mixed model using the total number of bat passes per night per site as a response variable with a Poisson or a negative binomial error distribution (Zuur *et al.*, 2009). Light treatment (composed of 3 factors: unlit, part-night lighting, and full-night lighting) and the land-use covariables (VIF < 3) were included in the models as fixed effects; the covariables were the proportion of forested, impervious, and open areas within a 250-m radius buffer around each sample site. We selected this scale as it represented the limit beyond which there were no differences in land-use composition between the 3 light treatments (Table S1). We also tested the effect of land-use within a 50-m radius buffer around each sample site, which corresponds to the average detection distance of each species (Barataud, 2012), but none of the land-use covariables were significant at this spatial scale. The average night temperature (°C), the

moon phase (composed of 3 factors: ascending, descending or absent), Julian date, and the time of sunset were also included as fixed effects in the models. As random effects, we included the identification number of the pair for each site, which was nested into the identification number of the municipality in which each pair was located. The former random effect allowed the pair-wise comparison of bat activity among light treatments, whereas the purpose of the latter was to take the similarities in environmental management between nearby pairs into account. For each species, we selected the best model by removing each fixed effect one by one and comparing the residual deviance of the subsequent models with a type II ANOVA associated with a chi-squared test (Table S2; Zuur *et al.*, 2009). Model validation was carried out by visual inspection of the patterns of the model residuals (Zuur *et al.*, 2009). All analyses were performed in R 3.15 with the 'MASS' package and the 'glmmPQL' function.

Results

Bat monitoring

A total of 57 341 bat passes belonging to 6 species and 2 species groups were recorded in the 72 study sites, and the most abundant species was the common pipistrelle bat, *P. pipistrellus*, representing 83 % of the observations (Table 1). The least abundant species were *Plecotus* spp. (481 bat passes) and *Pipistrellus nathusius* (595 bat passes) although they were present in 50 % and 30 % of the 72 sites, respectively.

Effect of light treatment on bat activity

In comparison with the unlit control treatment, full-night lighting had a significant negative effect on *Myotis* spp. ($P < 0.05$; Table 2; Fig. 2A) and a nearly significant negative effect on *Plecotus* spp. ($P = 0.08$; Table 2; Fig. 2B). In contrast, full-night lighting had a significant positive effect on *P. pipistrellus* ($P < 0.001$; Table 2; Fig. 2C), *Pipistrellus kuhlii* ($P < 0.001$, Table 2;

Table 1 Description of the bat dataset for each species from the 72 sites including flight behavior (FF = fast-flying, SF = slow-flying), the number of bat passes, the final model, and the response variable distribution selected for each species (NB = negative binomial, θ = overdispersion coefficient)

Flight behavior	Species	No. of bat passes	Final model formula	Distribution
FF	<i>Pipistrellus pipistrellus</i>	46 314	Light treatment	Poisson
	<i>Eptesicus serotinus</i>	3305	Light treatment +% open areas	Poisson
	<i>Pipistrellus kuhlii</i>	1156	Light treatment	Poisson
	<i>Nyctalus leisleri</i>	976	Light treatment +% open areas	Poisson
	<i>Nyctalus noctula</i>	844	Light treatment +% forest +% open areas	NB ($\theta = 6.1$)
	<i>Pipistrellus nathusius</i>	595	Light treatment +% forest +% impervious areas +mean T °C	NB ($\theta = 5$)
SF	<i>Myotis</i> sp.	3670	Light treatment +% forest +% open areas +% impervious areas	Poisson
	<i>Plecotus</i> sp.	481	Light treatment +mean T °C	NB ($\theta = 5.1$)

Fig. 2D), and *Nyctalus leislerii* ($P < 0.01$; Table 2) and a nearly significant positive effect on *P. nathusius* ($P = 0.08$; Table 2). No effect of full-night lighting on *Eptesicus serotinus* and *Nyctalus noctula* was found (Table 2).

Similar to the full-night lighting treatment, part-night lighting sites also had significantly less *Myotis* spp. activity ($P < 0.01$) and significantly more activity by *P. kuhlii* ($P < 0.001$), *P. nathusius* ($P < 0.01$), and *N. leislerii* ($P < 0.05$; Table 2) than the unlit control sites (Table 2; Fig. 2). For these 4 species, there were no differences between the part-night and full-night lighting sites (Table 2), but for the 3 remaining species, the effect of part-night lighting differed from the effect of full-night lighting. The activity of *P. pipistrellus* on the part-night lighting sites was half of that under full-night lighting ($P < 0.001$; Fig. 2C), and there was no significant difference in bat activity between the unlit and part-night lighting sites (Table 2; Fig. 2C). In contrast, there was significantly more *Plecotus* spp. ($P < 0.01$; Table 2; Fig. 2B) and *N. noctula* ($P < 0.001$; Table 2) activity on part-night lighting sites than on the unlit or full-night lighting sites.

Discussion

To our knowledge, this study is the first to empirically test the effectiveness of part-night lighting schemes on the mitigation of the impacts of artificial lighting on the activity of a bat assemblage. Given that part-night lighting schemes have been in place for several years in our study site, our *in situ* experiment provided a unique opportunity to characterize how bat species have adapted their foraging and commuting behaviors to this mitigation measure.

Our study examined the effects of only high-pressure sodium (HPS) vapor lamps, which are the most commonly used type of lamp in European public lighting (Eisenbeis, 2006). Due to the low emissions of short wavelength UV, HPS vapor lamps attract fewer insects and, therefore, fewer bats than mercury vapor lamps (Blake *et al.*, 1994; Eisenbeis, 2006). Nevertheless, insect traps illuminated by HPS lamps still catch 27 times the insects caught by traps under dark conditions, and the attraction effect extends to 40 m from a light source (Perkin *et al.*, 2014). Consistent with other studies, our experiment showed that the streetlights were creating additional foraging opportunities for the fast-flying *Pipistrellus* spp. and *Nyctalus* spp. (Rydell, 1992; Rydell 2006) while reducing the availability of foraging patches for the slow-flying *Myotis* spp. and *Plecotus* spp. (Kuijper *et al.*, 2008; Stone *et al.*, 2009). Similar bat response patterns to artificial lighting have been observed even under low light intensities (Lacoeuilhe

Table 2 Estimates and standard errors for part-night and full-night lighting treatments when the unlit control treatment (A and B, respectively) and the full-night lighting treatment (C) are used as the intercept of the final model for the 8 species studied (** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, **** $P = \pm 0.05$). Complete models for each species can be found in Table S3

	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus kuhlii</i>	<i>Pipistrellus nathusius</i>	<i>Nyctalus leislerii</i>	<i>Nyctalus noctula</i>	<i>Eptesicus serotinus</i>	<i>Myotis</i> sp.	<i>Plecotus</i> sp.
Light treatment								
(A) Part-night vs. Unlit	0.15 (0.17)	1.27 (0.33)***	1.80 (0.51)**	3.10 (1.18)*	1.18 (0.25)***	-0.68 (0.40)****	-0.91 (0.28)**	0.67 (0.24)**
(B) Full-night vs. Unlit	0.93 (0.19)***	1.25 (0.27)***	0.86 (0.70)****	2.48 (0.59)**	0.03 (0.50)	-0.23 (0.40)	-2.40 (1.22)*	-0.74 (0.40)****
(C) Part- vs. Full-night	-0.78 (0.22)**	0.01 (0.41)	0.94 (0.58)	0.73 (0.93)	1.14 (0.50)*	-0.44 (0.52)	1.49 (1.22)	1.46 (0.47)**

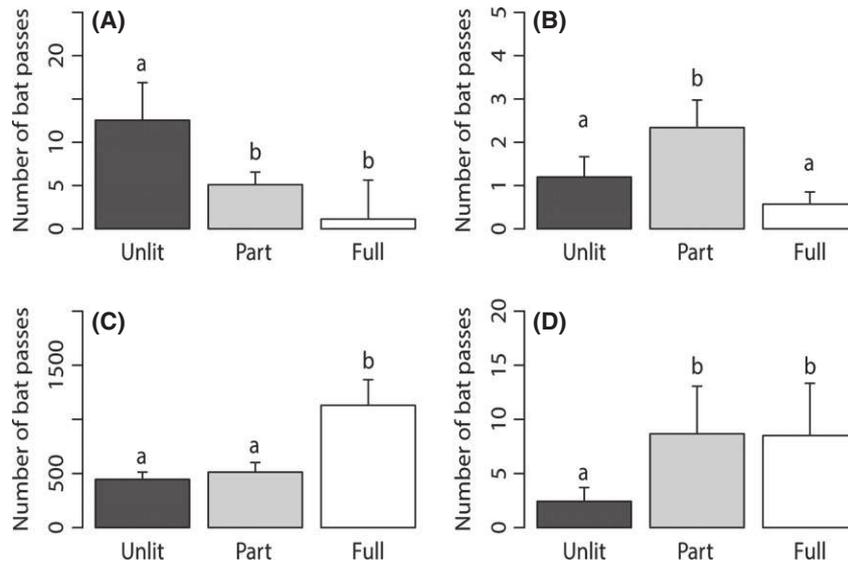


Fig. 2 Predicted number of bat passes per night and the associated standard errors under unlit, part-night, and full-night lighting treatments for (A) *Myotis* sp., (B) *Plecotus* sp., (C) *Pipistrellus pipistrellus*, and (D) *Pipistrellus kuhlii*. a and b refer to the light treatments that are not significantly different from one another.

et al., 2014), including energy-efficient light-emitting diode (Stone *et al.*, 2012).

It is important to note that the increased foraging opportunities induced by artificial lighting for fast-flying bats may not be stable because the massive attraction of insect species to streetlights is likely to have significant impacts on their long-term demography (Eisenbeis, 2006; Moore *et al.*, 2006). Common macro-moths have experienced major declines in the UK in recent decades (Conrad *et al.*, 2006), and it has been hypothesized that urban areas and their associated sky glow may act as ecological sinks, depleting the surrounding landscapes of moth species (Bates *et al.*, 2014). Cascading effects of these declines may be expected in the long term (Van Langevelde *et al.*, 2011).

In our study, the effect of part-night lighting differed among species and highlights the importance of addressing the efficacy of a mitigation measure at the community level. For the 3 fast-flying species, *P. kuhlii*, *P. nathusius* and *N. leislerii*, and the slow-flying *Myotis* spp., part-night lighting schemes did not drastically change the overall level of activity around streetlights. This suggests that current part-night lighting schemes do not coincide with the activity window of these species (Gaston *et al.*, 2012). This is particularly important for the light-sensitive *Myotis* spp., which were significantly less active under both light treatments than on the unlit control sites. Slow-flying species, such as *Myotis* spp., are important conservation targets as they are particularly sensitive to habitat loss and fragmentation (Safi & Kerth, 2004; Frey-Ehrenbold *et al.*, 2013).

Disturbances to bat commuting routes induced by artificial lighting can significantly impact the fitness and reproductive success of light-sensitive species by increasing the distance between roosts and suitable foraging sites (Stone *et al.*, 2009). Our results suggest that current part-night lighting schemes do not limit night-scape fragmentation for this genus.

Consistent with our hypothesis, there was no difference in overall bat activity between part- and full-night lighting sites for the 3 fast-flying species, *P. kuhlii*, *P. nathusius*, and *N. leislerii*, which are known to emerge at dusk (Jones & Rydell, 1994; Rydell, 2006). However, *P. pipistrellus* did not respond similarly to the other fast-flying species; it exploited the part-night lighting sites 2 times less than the full-night lighting sites even before the streetlights were extinguished (Fig. 3). This is surprising because this species appears to have foraging behaviors similar to other fast-flying species (Rydell, 2006). Once they have identified suitable foraging areas, individual bats show strong site-fidelity over time (Bonaccorso *et al.*, 2005; Hillen *et al.*, 2009). As part-night lighting schemes have been in place for several years in the study area, *P. pipistrellus* individuals may have identified the streetlights used in part-night lighting as less suitable foraging sites than the full-night lighting sites. This would be especially likely during the reproduction period (as in our study) when the energetic costs of reproduction influence female foraging strategies (Racey & Swift, 1985; Barclay, 1989; Rydell, 1989; Duvergé *et al.*, 2000).

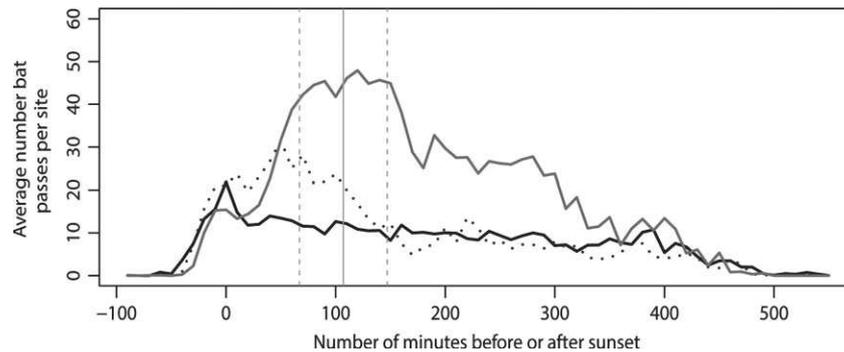


Fig. 3 Average number of *Pipistrellus pipistrellus* bat passes recorded per site per 10-min period before or after sunset (raw data) under unlit (black line), part-night (dotted line), and full-night (gray line) lighting treatments. The vertical gray line represents the average time (with the range in gray-dashed lines) at which streetlights were switched off in the part-night lighting schemes.

In contrast, part-night lighting had a significant positive effect on the slow-flying *Plecotus* genus with more activity on part-night lighting sites compared to both unlit and full-night lighting sites. This suggests that current part-night lighting schemes overlap with part of its activity range. This finding is consistent with the literature as *Plecotus* spp. is one of the late-emerging bat taxa (Jones & Rydell, 1994; Rydell *et al.*, 1996). Furthermore, *Plecotus* spp. forages on prey, such as moths, by gleaning the vegetation or substrate surface (Rydell, 1992; Rydell *et al.*, 1996; Jones & Rydell, 1994). The attraction of insects to streetlights is often coupled with a 'fixation effect', meaning the insects stop flying and land on the ground or the surrounding vertical surfaces (Eisenbeis, 2006). They can even remain stationary within the illuminated area for several hours (Frank, 2006), so *Plecotus* spp. may be taking advantage of the stationary insects around streetlights once the lights have been turned off. A similar response was observed in *N. noctula*, but this species is a long-range echolocator, and its range of detection can extend up to a 100 m (Obrist *et al.*, 2004; Frey-Ehrenbold *et al.*, 2013). However, due to (i) the limited number of bat pass for this species and (ii) the level of uncertainty associated with the position of each bat pass, we must be cautious with these results.

Our study demonstrates that current part-night lighting schemes fail to overlap with the range of activity of 5 of the 8 bat species studied. This suggests that even if this mitigation measure limits CO₂ emissions and enhances energy savings, it is currently not an effective mitigation measure for biodiversity. However, further studies may confirm our results, especially for species such as *Plecotus* spp., *Myotis* spp., and *Nyctalus noctula* as the estimates from the full-night lighting treatment were associated with relatively large standard errors because of the low number of sites sampled ($n = 12$). For example, the fact that twice as many *Myotis* spp.

were recorded on part-night lighting sites as on full-night lighting sites could suggest a slightly beneficial effect of part-night lighting for this genus, but this difference was not significant due to the highly variable activity of *Myotis* spp. on the full-night lighting sites. Simulated part-night lighting scenarios have shown that streetlights must be switched off before 23:00 hours to coincide with a significant portion of the activity range of the light-sensitive *Rhinolophus ferrumequinum* (Day *et al.*, 2015). Therefore, part-night lighting schemes may become an efficient mitigation measure for *Myotis* spp. if implemented earlier at night. Starting part-night lighting schemes before 23:00 hours at the scale of an entire city or region would likely face resistance from the local inhabitants (Gaston *et al.*, 2012). However, this could be a valuable strategy along ecological corridors, such as urban parks and river banks, that would allow light-sensitive species to persist in urban and peri-urban environments (Jung & Kalko, 2010; Threlfall *et al.*, 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Results of the Kruskal-Wallis analysis of whether the proportions of the different land cover types around each study site were similar between the 3 light treatments across 6 spatial scales.

Table S2. Increase in the residual deviance of the model when removing each explanatory variable one by one calculated with a type II ANOVA with a chi-squared test (**Pr(>Chisq) < 0.001, **Pr(>Chisq) < 0.01, *Pr(>Chisq) < 0.05, . Pr(>Chisq) = ±0.05).

Table S3. Estimates and the associated standard errors, β , of all of the fixed effects selected for the final models for the 8 study species (**Pr < 0.001, **Pr < 0.01, *Pr < 0.05, . Pr = ±0.05). The estimates for the part-night and full-night lighting treatments are calculated in comparison with the unlit treatment (Intercept). Pseudo-R² values for the 8 final models were calculated by comparing the null and residual deviances from the null and final models, respectively (Zuur *et al.*, 2009).

Online Appendices

Table S1. Results of the Kruskal-Wallis analysis of whether the proportions of the different land cover types around each study site were similar between the 3 light treatments across 6 spatial scales.

	% forest	% agriculture areas	% impervious areas	% open areas
50	X² = 6.27, p = 0.04	X² = 5.49, p = 0.06	X² = 28.83, p < 0.0001	X² = 11.02, p = 0.004
100	X² = 6.43, p = 0.04	X² = 6.20, p = 0.05	X² = 24.90, p < 0.0001	X² = 13.21, p = 0.002
250	X ² = 1.89, p = 0.39	X ² = 4.22, p = 0.12	X² = 11.50, p = 0.003	X² = 9.39, p = 0.009
500	X ² = 1.68, p = 0.43	X ² = 4.10, p = 0.13	X ² = 4.84, p = 0.09	X ² = 5.32, p = 0.07
1000	X ² = 1.68, p = 0.43	X ² = 3.69, p = 0.16	X ² = 0.95, p = 0.62	X ² = 7.91, p = 0.02
2000	X ² = 0.11, p = 0.94	X ² = 2.20, p = 0.33	X ² = 0.64, p = 0.73	X ² = 15.03, p < 0.0001

Table S2. Increase in the residual deviance of the model when removing each explanatory variable one by one calculated with a type II ANOVA with a chi-squared test (***) Pr(>Chisq) < 0.001, ** Pr(>Chisq) < 0.01, * Pr(>Chisq) < 0.05, . Pr(>Chisq) = +/-0.05).

	Df	<i>P.pipistrellus</i>	<i>P.kuhlü</i>	<i>P.nathusius</i>	<i>N.noctula</i>
Light treatment	2	25.43***	8.50*	11.55 **	53.20***
% open surfaces	1	0.00	0.04	0.11	12.63***
% impervious surfaces	1	0.01	2.95.	8.85 **	0.06
% forest	1	2.83	2.29	10.05**	9.79**
Time after sunset	1	0.08	0.02	0.46	1.01
Mean temperature (°C)	1	0.00	1.78	4.89*	0.11
Date	1	1.08	2.33	0.09	0.14
	Df	<i>N.leislerii</i>	<i>E.serotinus</i>	<i>Myotis sp.</i>	<i>Plecotus sp.</i>
Light treatment	2	2.36 .	3.59 .	11.99**	16.11**
% open surfaces	1	1.49 .	2.32 .	4.32*	2.11
% impervious surfaces	1	0.06	0.43	15.71**	1.07
% forest	1	1.65	0.28	4.17*	0.57
Time after sunset	1	0.19	0.59	0.07	2.04
Mean temperature (°C)	1	0.70	0.21	1.07	5.12*
Date	1	0.01	0.76	1.08	0.96

Table S3. Estimates and the associated standard errors, β , of all of the fixed effects selected for the final models for the 8 study species (** $P < 0.01$, * $P < 0.05$, . $P = +/- 0.05$). The estimates for the part-night and full-night lighting treatments are calculated in comparison with the unlit treatment (Intercept). Pseudo- R^2 values for the 8 final models were calculated by comparing the null and residual deviances from the null and final models, respectively (Zuur *et al.*, 2009).

	<i>P. pipistrellus</i>	<i>P. kuhlii</i>	<i>P. nathusius</i>	<i>N. leisterii</i>	<i>N. noctula</i>	<i>E. serotinus</i>	<i>Myotis sp.</i>	<i>Plecotus sp.</i>
Pseudo-R^2	0.35	0.32	0.17	0.44	0.44	0.23	0.58	0.32
Light treatment :								
<i>Intercept-Unlit</i>	6.10 (0.14)	0.89 (0.42)	-1.29 (0.54)	-1.92 (1.19)	0.02 (0.52)	3.57 (0.35)	2.54 (0.38)	0.18 (0.33)
<i>Part-night</i>	0.15 (0.17)	1.27 (0.33) ***	1.80 (0.51) **	3.10 (1.18) *	1.18 (0.25) ***	-0.68 (0.40) .	-0.91 (0.28) **	0.67 (0.24) **
<i>Full night</i>	0.93 (0.19) ***	1.25 (0.27) ***	0.86 (0.70) .	2.09 (0.59) **	0.03 (0.50)	-0.23 (0.40)	-2.40 (1.22) *	-0.74 (0.40) .
% forest	/	/	-0.04 (0.01) **	/	-0.09 (0.02) **	/	0.02 (0.01).	/
% open surface	/	/	/	-0.17 (0.05) **	-0.02 (0.01) .	0.04 (0.02) *	0.08 (0.04)*	/
% imperv. surface	/	/	-0.12 (0.05) **	/	/	/	0.1 (0.02) ***	/
Mean temperature	/	/	0.33 (0.14) *	/	/	/	/	0.06 (0.08)

Discussion & Perspectives

This study revealed that current part-night lighting schemes, with streetlights turning-off at midnight (i.e. streetlight extinction), were unlikely to effectively mitigate the impacts of nighttime artificial lighting on most bat species. This result confirmed the hypothesis that the timing of streetlight extinction does not correspond to the peak of activity of most nocturnal species (Gaston et al. 2012). Our *in situ* experiment was however based on existing part-night lighting schemes and we could not control for the timing of part-night lighting. Thus, investigating the effect of the timing of part-night lighting on bat activity would be worth further investigations in order to determine whether there is an optimal time schedule for streetlight extinction. Contrary to traditional streetlights, LEDs technologies allow controlling and manipulating streetlights parameters such as illuminance, spectrum and duration of lighting (Schubert & Kim 2005; Kyba et al. 2014b). These types of lamps can also be associated to motion sensors that drive the adaptation of brightness according to the vicinity of pedestrians and vehicles. In this context, it would be interesting to do a similar experiment with LEDs in order to i) test the effect of different timing of part-night lighting, and ii) examine the effect of lighting modulation through the night via motion sensors on bat activity.

Additionally, as insect abundance and richness are key components of ecosystems (Conrad et al. 2006), it would be interesting to study the effect of part-night lighting on insects. Although the majority of insect biomass presents a peak of activity at dusk (Jetz et al. 2003), some taxa such as macromoths appear to be active later at night (Figure 11; Rydell et al. 1996). Furthermore, the “vacuum cleaner” effects of streetlights may attract insects and keep them active even after their normal window of activity. Hence, part-night lighting schemes may actually be effective in reducing the streetlight-induced mortality of insects for at least a part of the night. If so, part-night lighting landscapes may present a higher abundance of insect

prey than full-night lighting ones. In this context, part-night lighting schemes may positively influence bat occurrence and long-term population trends at a landscape scale by increasing the abundance of prey.

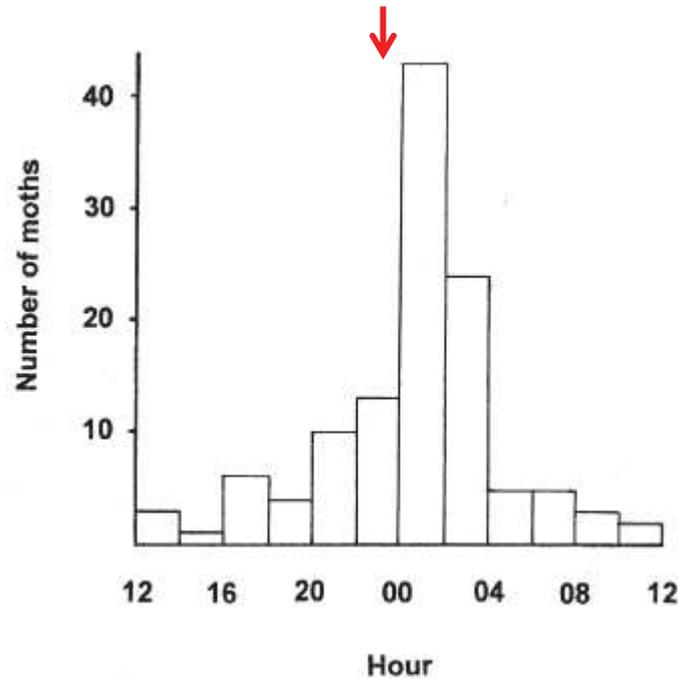


Figure 11. Histogram extracted from Rydell et al. (1996) showing the number of moths caught per hour in a in a Johnson-Taylor suction trap at their field site (the red arrow indicates the usual time of streetlight extinction).

In order to address this issue, we investigated the landscape-scale effect of part-night lighting schemes on bat occurrence using the biological data of the “Vigie Chiro” program that has been running since 2006 in the Park (Vernet 2014). This work was specifically done by Arthur Vernet (Vernet 2014), a master student who I co-supervised with Isabelle Le Viol, Christian Kerbiriou and Julie Maratrat from the Natural Park of the French Gâtinais. Part-night lighting schemes had a positive effect on the activity of *P. kuhlii/nathusius*, with significantly more bat passes along car transects located in part-night lighting areas compared to transects located in full-night lighting areas (Figure 12). However, we did not find any effect of the lighting scheme for *P. pipistrellus*, *Eptesicus/Nyctalus* and *Myotis sp.* This exploratory analysis was done on a relatively small study area and with a small number of

spatial replicates (10 road circuits). Thus, it would be interesting to increase the spatial extent of this analysis to a regional or even a national scale in order to assess whether part-night lighting schemes can significantly influence bat spatial distribution and population trends.

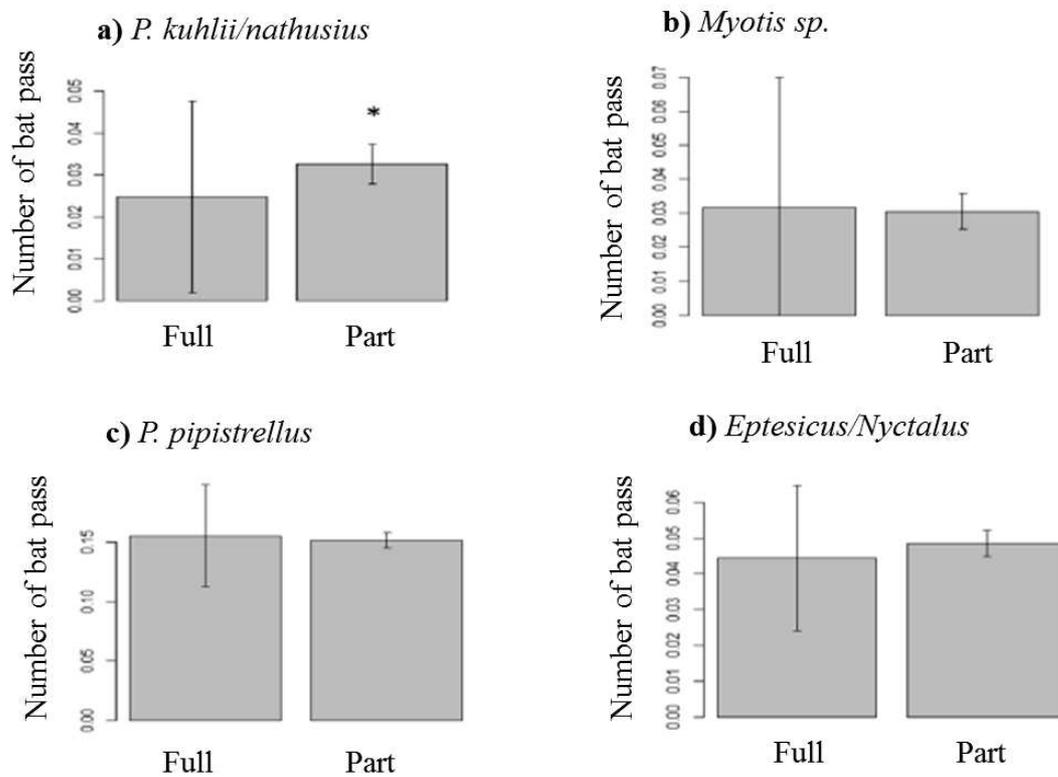


Figure 12. Average number of bat passes/car transect (raw estimates) located in full and part-night lighting areas for **a)** *P. kuhlii/nathusius*, **b)** *Myotis sp.*, **c)** *P. pipistrellus* and **d)** *Eptesicus/Nyctalus* (* $P < 0.05$).

The results of this chapter revealed that limiting the temporal extent of lighting was unlikely to effectively reduce the negative impacts of outdoor lighting on light-sensitive species. Thus, in the next chapter, we investigated whether limiting the spatial extent of artificial lighting and enhancing darkness in space could be a better option.

CHAPTER 3:

Limiting the spatial extent of artificial lighting along ecological corridors: Implications for outdoor lighting planning recommendations

Based on the paper:

Azam C, Le Viol I, Bas Y, Zisis G, Vernet A, Julien J-F, Kerbiriou C. Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity.

Ready for submission

Introduction

In 2013, the European commission adopted a “Green Infrastructure Strategy” to promote the development and protection of networks of natural and semi-natural areas in European urban and rural landscapes (EC 2013). As part of the European Union “Biodiversity Strategy for 2020”, the overall goal of this political engagement is to create a Trans-European Network for Green Infrastructure equivalent in its planification to the Trans-European Transport Network (EC 2013). Similarly, since 2010, French municipalities are asked to enhance, restore and conserve the ecological integrity of green areas and aquatic ecosystems in their land-use planning strategies (“Trame Verte et Bleue”, Grenelle Environment 2010).

The aim of these policies is to implement functional networks of ecological corridors that facilitate the movements of plant and animal populations in fragmented areas (i.e. restoration of landscape connectivity; Ricketts 2001). Landscape connectivity is determinant for the persistence of a species in a given area as it influences the availability and accessibility of suitable resource patches for the individuals of a given population. It also drives species metapopulation dynamics at a landscape scale (source-sink and colonization-extinction dynamics; Taylor et al. 1993). Finally, it can dramatically influence the dispersal success of individuals over large spatial scales which in turn have important implications for gene flows (Baguette et al. 2013). However, none of these policies that tend to restore landscape connectivity, propose recommendations for artificial lighting management within and along these ecological corridors. Considering that 30 % of vertebrates and 60 % of invertebrates are nocturnal (Hölker et al. 2010b), it is likely that these policies will be ineffective for a substantial part of biodiversity if not planned concomitantly with the spatial planning of outdoor lighting.

The 2 previous chapters highlighted the importance of restoring darkness in human-inhabited landscapes and revealed that turning-off streetlights in the middle of the night was unlikely to effectively reduce the negative impacts of outdoor lighting on light-sensitive species. Thus, this last chapter intentionally focuses on the spatial distribution of artificial lighting in human-inhabited landscapes. In particular, I intended to estimate how far streetlights should be separated from structural connectivity elements such as hedgerows and forest edges to allow their use by light-sensitive bat species. However, the propagation of artificial lighting in the environment may not only be influenced by the position of streetlights, but also by the directionality of the luminous flux they emit. Therefore, I additionally investigated how the level of light illuminance received by structural connectivity elements influenced bat activity. The aim of this approach was to estimate the minimum level of light trespass that should be avoided to restore darkness along structural connectivity elements.

Using the same *in situ* experimental set up in the Natural Park of the French Gâtinais, we first estimated the distance of impact of streetlights on the activity microchiropteran bats. We secondly investigated whether bats were more sensitive to the illuminance received by vertical surfaces than horizontal ones (vegetation versus ground), and if there was an illuminance threshold below which artificial lighting did not influence bat activity. Finally, as half of the territory of the Natural Park was under part-night lighting schemes, we tested whether the distance of impact of streetlights remained once they were turned off. The overall goal of this chapter was i) to elaborate practical recommendations for the spatial planning of outdoor lighting in and around ecological corridors in human-inhabited landscapes, and ii) to define lighting criteria that could be implemented in connectivity modelling.

Article 3

Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity.

List of author: Clémentine Azam¹ cazam@mnhn.fr, Isabelle Le Viol¹ ileviol@mnhn.fr, Yves Bas¹ ybas@mnhn.fr, Georges Zissis² georges.zissis@laplace.univ-tlse.fr, Arthur Vernet³ arthur.ver@hotmail.fr, Jean-François Julien¹ jfjulien@mnhn.fr, Christian Kerbiriou¹ kerbiriou@mnhn.fr

Institutional affiliations:

¹ National Museum of Natural History, 55 rue Buffon,

Center for Ecology and Conservation Science, UMR7204-MNHN-CNRS-UPMC, 75005

Paris, France

² Head of Light & Matter Research Group, Laplace Institute, University Paul Sabatier, 31000

Toulouse, France

³ Parc Naturel Régional du Gâtinais Français, 20 boulevard du Maréchal Lyautey, 91490

Milly-la-Forêt, France

Corresponding author: Clémentine Azam cazam@mnhn.fr

Running title: Effects of outdoor lighting on bats

Keywords: light pollution, distance of impact, illuminance, Chiroptera, ecological corridors, urbanization, land-use planning

Abstract

Light pollution affects major proportions of global land surface with important implications for biodiversity and ecosystem dynamics. Thus, there is an urgent need to elaborate outdoor lighting strategies that reduce its adverse impacts on biodiversity. In particular, the position of light sources in the landscape, its duration via part-night lighting, and the level of illuminance on the vegetation surrounding streetlights are crucial parameters that can be controlled to enhance dark refuges in human-inhabited landscapes.

Through a paired, *in situ* experiment, we estimated the distance of impact of streetlights and characterized the effect of light illuminance on the activity of 6 species and 2 genera of bats. We selected 27 pairs composed of 1 lit site and 1 control dark site, and located in areas practicing either part-night or full-night lighting. We recorded bat activity at 0, 10, 25, 50 and 100 m, and measured vertical and horizontal light illuminance at each of the 5 distance steps (range = 0.1 - 30.2 lx).

The negative effect of streetlights was detectable at 0 and 10 m for *Myotis sp.* and at 25 and 50 m for *Eptesicus serotinus*, while the attraction effect of streetlights was detectable at 0 m for *Pipistrellus kuhlii* and *Pipistrellus nathusius*, until 10 m for *Pipistrellus pipistrellus* and *Nyctalus leisleri*, and until 100 m for *Nyctalus noctula*. The effects of streetlights on *Myotis sp.* and *Nyctalus sp.* remained after the lamps were turned off, contrary to the attraction effect on *Pipistrellus sp.*

Light illuminance had a negative effect on *Myotis sp.* even at illuminance values below 1 lx, and a contrasted effect on *E. serotinus*. It had a positive effect on all the other species, although a peak of activity was observed between 1 and 5 lx for *P. pipistrellus*, *N. leisleri*.

Synthesis and applications. This study highlights the additional habitat loss and fragmentation induced by streetlights and the necessity of enhancing dark refuges in human-inhabited landscapes. Thus, we recommend to separate streetlights from ecological corridors by at least 50 m and to avoid vertical light trespass beyond 0.1 lx.

Introduction

Considering current degree of urbanization worldwide, the mitigation of its impacts on biodiversity has become a major challenge in conservation biology and land-use planning (Grimm et al. 2008a). However, urbanization process is also associated to the emission of environmental stressors such as chemical, noise and light pollutions which can diffuse way beyond urban and suburban landscapes and affect a substantial part of surrounding ecosystems (Grimm et al. 2008b). In particular, light pollution is a global change affecting 23% of global land surface and 88% of Europe, and spreading at an annual rate of 6% worldwide (Hölker et al. 2010a; Falchi et al. 2016).

Ecological light pollution alters the natural light cycles that both diurnal and nocturnal organisms use as a cue to synchronize their biological rhythms with their environment. This desynchronization has important consequences for individual fitness, sexual selection, and reproductive success of animal populations (Boldogh et al. 2007; Nordt & Klenke 2013; van Geffen et al. 2015a). Furthermore, species responses to artificial lighting are driven by attraction/repulsion behaviors, and resulting spatial distribution of species may be influenced at various spatial and temporal scales (Mathews *et al.* 2015; Azam *et al.* 2016). Taken together, the effect of light pollution on organisms likely impacts the spatiotemporal dynamics of biological communities and whole ecosystems (Minnaar et al. 2015; Macgregor et al. 2016). Thus, developing artificial lighting strategies that minimize the negative impacts on biodiversity while meeting social and safety requirements for humans represent a major challenge in land-use planning (Gaston et al. 2012).

As they are nocturnal and directly exposed to light pollution, microchiropteran bats are good candidates to explore the effect of artificial lighting on nocturnal biodiversity. As long-lived insectivorous species with a slow reproductive rate, they are good indicators of the response

of biodiversity to anthropogenic pressures and important ecosystem services delivers (Jones *et al.* 2009; Charbonnier *et al.* 2014). Bat responses to artificial lighting vary among species according to their foraging strategies and flight abilities (Jones & Rydell 1994). Slow-flying species adapted to prey on insects in cluttered vegetation, such as *Rhinolophus spp.*, *Myotis spp.*, and *Plecotus spp.*, avoid illuminated areas due to an intrinsic perception of increased predation risk (Rydell *et al.* 1996). This avoidance behavior has been detected regardless of the lamp spectrum (Stone *et al.* 2015a) and even at low level of light illuminance (Lacoeuilhe *et al.* 2014). In contrast, fast-flying species adapted to forage insects in the open air, such as *Pipistrellus spp.* and *Nyctalus spp.*, are suggested to benefit locally from new and predictable foraging opportunities provided by streetlights (Rydell 1992; Blake *et al.* 1994b), which attract a large portion of the surrounding insect biomass (Perkin *et al.* 2014a). Nevertheless, landscape-scale level of light pollution negatively affects bat occurrence, regardless of the species foraging strategy (Azam *et al.* 2016). Such large-scale negative effect may be partly due to the “barrier effect” artificial lighting can induce on individuals’ movements and gap-crossing behaviors in illuminated landscapes (Stone *et al.* 2009; Hale *et al.* 2015).

Current land-use planning policies tend to restore biodiversity dynamics in human-inhabited landscapes by enhancing functional networks of ecological corridors that connect patches of natural and semi-natural remnants, and ensure animal movements and metapopulation dynamics (Minor & Urban 2008). As for many other organisms, bats’ persistence in both urban and rural landscapes is highly reliant on the presence of structural connectivity elements such as tree lines, hedgerows and riverbanks that increase landscape connectivity (Hale *et al.* 2012; Lintott *et al.* 2015). However, there are at the moment no recommendations for artificial lighting management in and around ecological corridors, although essential to ensure their effective use by nocturnal species.

Limiting the impacts of light pollution on biodiversity including bats requires to manage artificial lighting through 5 integrated levers of action that emphasize *i*) the spatial arrangement of light sources in the landscape; *ii*) the reduction of light trespass into areas that are not intended to be lit; *iii*) the limitation of the duration of lighting; *iv*) the reduction in the illuminance emitted by light sources; and *v*) the adaptation of the spectral composition of the lamps (Gaston et al. 2012; Kyba et al. 2014b). However, although particular attention has been given to the ecological impacts of lamp spectral composition (Stone et al. 2015b; Lewanzik & Voigt 2016) and of lighting duration (Azam et al. 2015; Day et al. 2015), the impacts of the position and the orientation of artificial light sources on biodiversity are unknown. In the present study, with an *in situ* paired experiment, we *i*) estimated how far should streetlights be separated from landscape structural connectivity elements to allow their use by bats; *ii*) tested whether such impacts remained once streetlights were switched-off; and *iii*) characterized the effect of light illuminance received by the horizontal and vertical surfaces surrounding streetlights on the activity of 6 species and 2 genera of bats.

Materials and methods

Study area

The field experiment was set up in a protected, 849-km² natural park (IUCN Protected Area Category VI). The park is located 60 km south of Paris, France and is comprised of 69 municipalities that average 12 km² in size. Part-night lighting schemes have been employed in 56 % of municipalities for at least two years. These schemes are designed to turn off all public streetlights (i.e. streetlight extinction) from midnight (+/- 1 hour) to 5 AM. Arable lands represent 58 % of the area, and forests comprise 31 % (Figure 13a). Currently, urban areas make up 8 % of the park, but the entire region is subject to pressures from urbanization due to its vicinity to the capital.

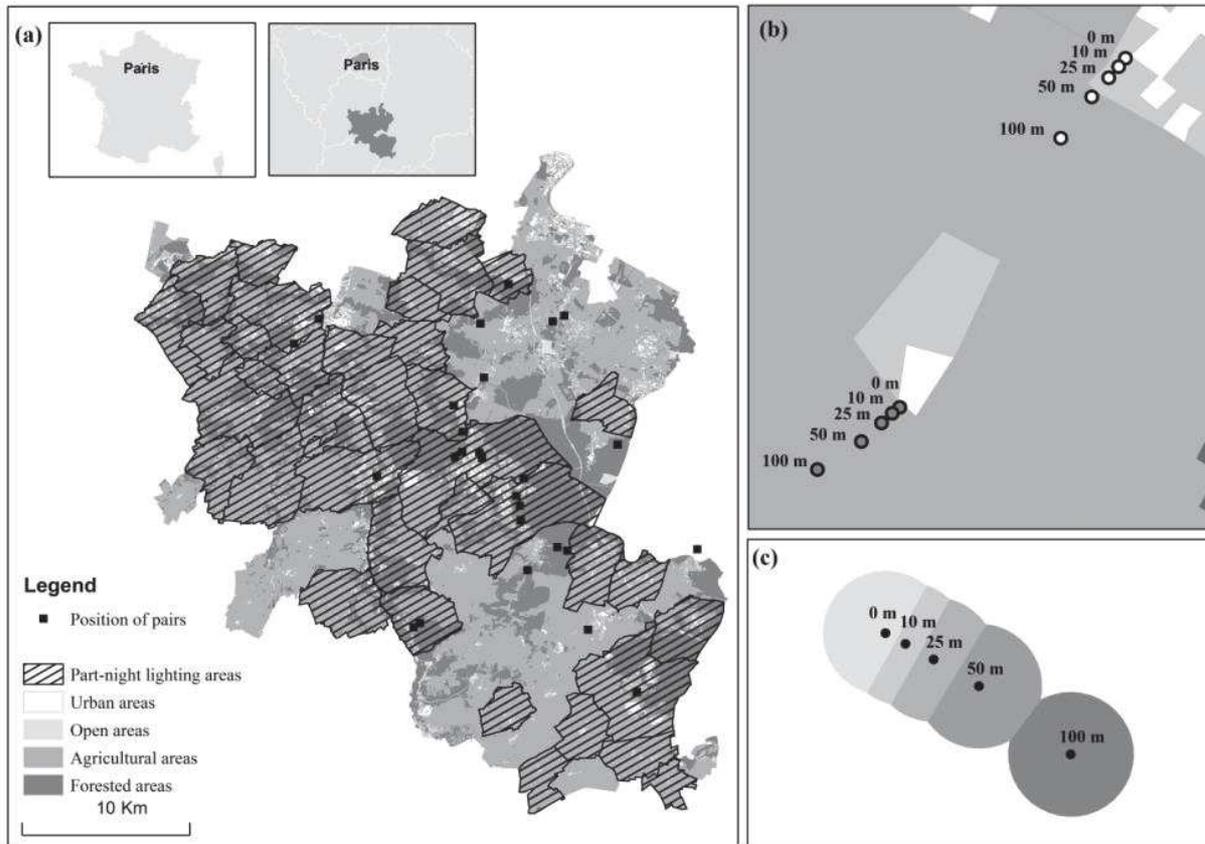


Figure 13. Presentation of the study area and the sampling design with (a) the position of the 27 pairs (lit/dark) with respect to the local administrations practicing part-night lighting and the regional land-uses; (b) the example of one pair composed of 1 lit site (white dots) and 1 dark site (grey dots) containing respectively 5 recordings stations located at 5 different distance steps from the streetlight and equivalent dark control (land-uses correspond to the legend in 1a); and (c) the representation of the area sampled by each recording station for *Pipistrellus sp.* (detection radius of 30 m).

Sampling design

We selected 27 study locations composed of 1 lit site and a paired, dark control site; 19 pairs were located in administrations practicing part-night lighting schemes, and 8 were located in municipalities with full-night lighting (Figure 13a). Lit sites were illuminated by 1 high-pressure sodium (HPS) vapor streetlight (average intensity = 16.7 lx; range = 6 - 42 lx) and dark control sites were separated from their paired lit site by approximately 250 m. The 2 sites of each pair were located in a similar habitat and set along a same bat commuting route, such as a forest edge or a hedgerow (Walsh & Harris 1996). They were also positioned away from

town cores and at similar distances from linear elements, such as roads and streams (See Table S1 for details on multicollinearity issues).

Both lit and dark sites were composed of 5 recording stations located at 0, 10, 25, 50 and 100 m from the streetlight (*i.e.* 10 recording stations per pair; Figure 13b). At each of the 5 recordings stations, we measured vertical and horizontal illuminance (lx) with a luxmeter (Digital Lx Tester YF-1065) fixed to a tripod of 1.20 m height (Fig. S1). Vertical illuminance refers to the luminous flux received by a 1 m² vertical surface such as trees and hedgerows while horizontal illuminance refers to the luminous flux received by a 1 m² horizontal surface such as roads and grounds.

Bat monitoring

Fieldwork was carried out *i)* from the 1st of May to the 07th of July, which corresponds to the seasonal peak of activity, and which is recommended by the French national bat-monitoring program “Vigie-Chiro” (<http://vigienature.mnhn.fr/>); *ii)* when weather conditions were favorable, *i.e.*, no rain, low wind speed (< 7 m/s) and temperatures higher than 12°C; *iii)* between the third and the first quarter moon to limit the interaction between natural and artificial lighting (Saldaña-Vázquez & Munguía-Rosas 2013).

Bat activity was sampled at each recording station with a SM2BAT (<http://www.wildlifeacoustics.com/>) which automatically recorded all ultrasound (high pass filter set at 12 KHz) with SMX-US omnidirectional microphones. The 10 recording stations of each pair were simultaneously sampled on the same night from 30 minutes before sunset to 30 minutes after sunrise, allowing the direct comparison of bat activity between the lit site and its paired dark control site at each of the 5 distance steps tested. Ambient temperature was also recorded every 30 minutes with an EL-USB-1 temperature data-logger (Lascar Electronics).

We used the software SonoChiro© (Bas *et al.* 2013) to automatically classify the echolocation calls to the most accurate taxonomic level possible. At each recording station, we measured a number of bat passes per species which is defined as the occurrence of a single or several echolocation calls of a same bat species during a 5-second interval. We then validated the software classification by screening all ambiguous calls with Syrinx software version 2.6 (Burt 2006). Identification was possible to the species level in all but two genera, *Plecotus spp.* and *Myotis spp.*, due to uncertainties in the acoustic identification at the species level (Obrist, Boesch & Fluckiger 2004). Overlap in the detection volume of the 5 recording stations occurred within sites depending on species detectability (Figure 13c; Barataud 2015). Thus, a bat pass of a same species that was simultaneously detected by 2 or more stations (in milliseconds) was associated to the station that recorded the highest number of bat calls since it corresponded most probably to the microphone that was closer to the transiting bat. Then, we applied for each species a correction on the number of bat passes to take into account subsequent uneven sampling volume among recording stations (Figure 13c; See details in Fig. S2).

Statistical analysis

Distance of impact of a streetlight on bat activity

For each species, we examined the effect of the streetlight on its activity at the 5 distance steps before and after streetlight extinction. First, we did generalized linear mixed models (GLMMs) using the number of bat passes before streetlight extinction as the response variable, and including as a fixed effect the interaction between the light treatment (2 factors: lit, dark) and the distance steps (5 factors: 0, 10, 25, 50, 100 m). Second, we did GLMMs using the number of bat passes after streetlight extinction as a response variable, and

including as a fixed effect the interaction between the lighting scheme (3 factors: dark, turned off, full-night lighting) and the distance steps.

In both models, we also included as fixed effects land-use covariables such as the proportion of impervious surface, forests and open areas within a 200 m buffer around each recording station, as well as the distance to the nearest road and to water (Table S1; see details: Azam *et al.* 2015). The average night temperature (°C), Julian date and the time of sunset were also included as fixed effects in both models. As random effects, we included the identity of the pair for each site, which was nested into the identity of the municipality in which each pair was located. The former random effect allowed the pair-wise comparison of bat activity among light treatment, whereas the purpose of the latter was to take the similarities in environmental management between nearby pairs into account. Following Zuur *et al.* 2009, we used either Poisson or negative binomial distribution to describe species responses in models (Table S2), and we selected one best model for before and after streetlight extinction with type II ANOVAs associated with chi-squared test (Table S3).

Effect of light illuminance on bat activity

For each species, we examined the effect of light illuminance on its activity before streetlight extinction. We did GLMMs using as a response variable the number of bat passes before streetlight extinction with a Poisson or a negative binomial error distribution. We included as a fixed effect the vertical illuminance measured at each recording station classified in 4 categories (dark; [0.1 – 1[; [1 – 5[; > 5 lx). We focused on vertical illuminance as it was a better predictor than horizontal illuminance (Table S4). We kept for each of these models the same covariables and random structure as in the previous analysis (Table S2). All the analyses were performed in R 3.15 with the ‘MASS’ package and the ‘glmmPQL’ function.

Results

Bat monitoring

A total of 118 950 bat passes belonging to 6 species and 2 groups of species were recorded among the 270 recording stations. The most abundant species was *P. pipistrellus* representing 80.7 % of the total dataset and the least abundant species were *Plecotus sp.* and *P. nathusius*, representing less than 1 % of the total dataset and only detected in 45 % and 21 % of the 270 recording stations, respectively (Table S2).

Distance of impact of a streetlight on bat activity

Before streetlight extinction, there was less activity of *Myotis sp.* and *E. serotinus* on lit sites compared to control dark sites at all distance steps tested (Figure 14a,b), although the difference was only significant at 0 and 10 m for the former ($P < 0.001$; Table 3), and at 25 and 50 m for the latter ($P < 0.001$; Table 3). In contrast, there was significantly more activity on lit sites than on control dark sites at 0 m for *P. kuhlii* ($P < 0.01$; Figure 14d) and *P. nathusius* ($P < 0.0001$; Table 3), at 0 and 10 m for *P. pipistrellus* ($P < 0.01$; Figure 14c), at 10 m for *N. leisleri* ($P < 0.0001$; Table 3), and finally at all distance steps for *N. noctula* ($P < 0.01$; Table 3). No significant effect of light treatment was observed for *Plecotus sp.* at any distance step tested.

After streetlight extinction, there was still significantly less activity of *Myotis sp.* at 0 and 10 m on turned off sites compared to control dark sites ($P < 0.001$; Figure 15a; Table 4), and no difference in the activity of this genus was observed between turned off and full-night lighting sites ($P > 0.05$; Table S5). In contrast, there was significantly more activity of *E. serotinus* and *N. leisleri* at 0 and 10 m, and of *N. noctula* at 0 and 50 m on turned off sites than on control dark sites ($P < 0.01$; Table 4). No significant difference in activity was recorded for *N. leisleri* and *N. noctula* between turned off and full-night lighting sites

(Table S5). However, the activity of *E. serotinus* was higher on turned off sites compared to full-night lighting sites until 50 m (Table S5). Finally, no significant difference in activity was recorded between turned off and control dark sites for *P. pipistrellus*, *P. kuhlii*, *P. nathusius* (Figure 14b; Table 4), except at 50 and 100 m for *P. nathusius* (Table 4). The activity remained significantly higher on full-night lighting sites compared to turned off sites at 0 and 10 m for *P. pipistrellus* and *P. kuhlii* (Figure 15b), and at 0, 10 and 50 m for *P. nathusius* (Table S5). No significant difference in activity was observed for *Plecotus sp.* between dark, turned off and full-night lighting sites, except at 25 m, where there was significantly less activity of this genus on turned off sites compared to dark sites (Table 4).

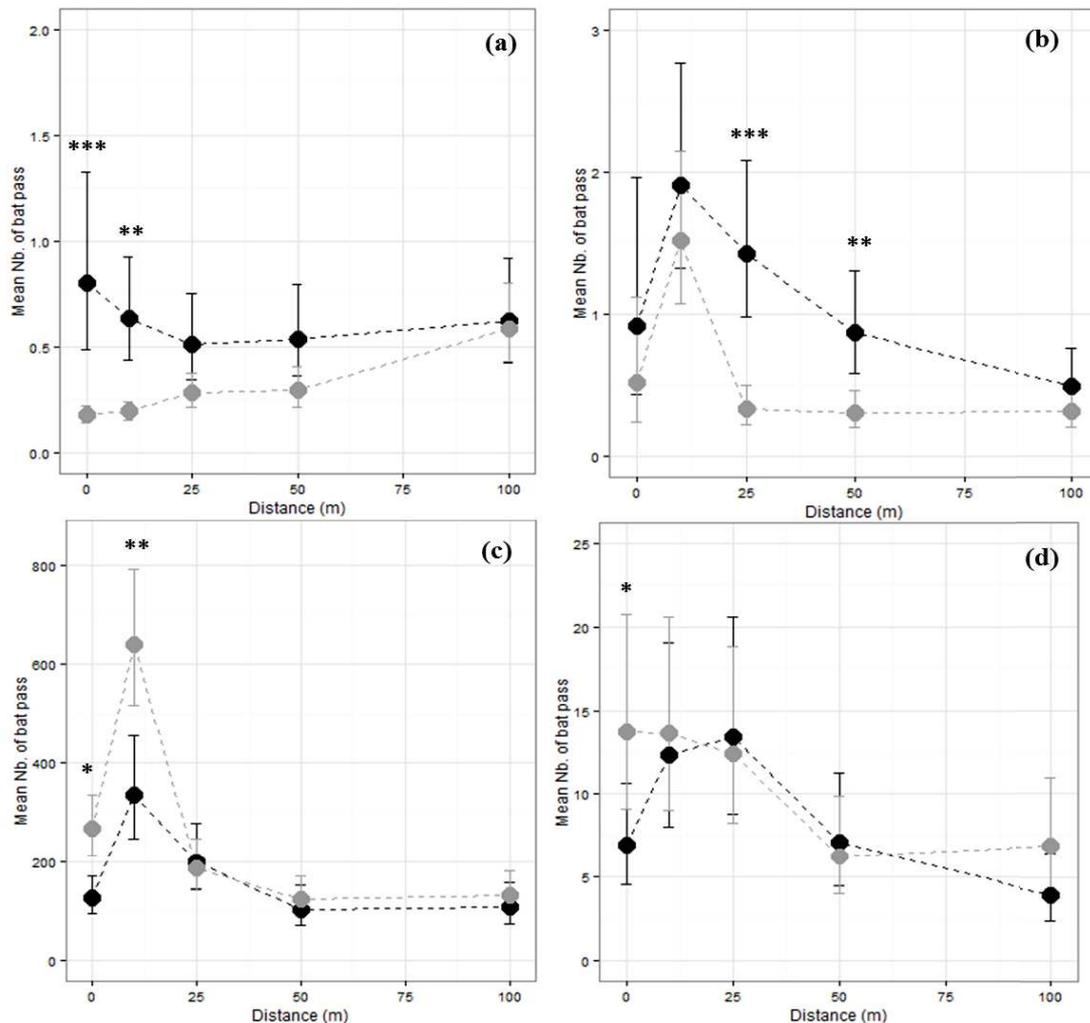


Figure 14. Predicted mean number of bat passes and associated standard errors of (a) *Myotis sp.*, (b) *E. serotinus*, (c) *P. pipistrellus*, (d) *P. kuhlii* at each distance step tested on lit sites (grey dots) and on control dark sites (black dots) before the time of streetlight extinction (‘***’ P < 0.0001; ‘**’ P < 0.001; ‘*’ P < 0.01).

Table 3. Estimates and standard errors per distance step for lit sites (Lit) compared to control dark sites (Dark) before streetlight extinction for the 6 species and 2 genera detected in our study.

Species	<i>Myotis sp.</i> (n = 2382)		<i>E. serotinus</i> (n = 4366)		<i>N. noctula</i> (n = 899)		<i>N. leisleri</i> (n = 465)	
Streetlight effect	-		-		+		+	
Pseudo-R²	0.63		0.31		0.44		0.15	
Lit vs. Dark	β	SE	β	SE	β	SE	β	SE
<i>Dist. 0 m</i>	-1.47***	0.45	-0.57.	0.32	1.80***	0.50	0.60	0.49
<i>Dist. 10 m</i>	-1.09**	0.44	-0.23	0.28	0.77.	0.37	1.54***	0.41
<i>Dist. 25 m</i>	-0.61	0.45	-1.44***	0.34	1.58***	0.37	0.45	0.34
<i>Dist. 50 m</i>	-0.59	0.44	-1.05**	0.35	1.04*	0.44	0.67	0.50
<i>Dist. 100 m</i>	-0.03	0.40	-0.46	0.38	1.83**	0.58	0.56	0.52

Species	<i>P. pipistrellus</i> (n = 35510)		<i>P. kuhlii</i> (n = 720)		<i>P. nathusius</i> (n = 210)		<i>Plecotus sp.</i> (n = 482)	
Streetlight effect	+		+		+		/	
Pseudo-R²	0.33		0.41		0.46		0.10	
Lit vs. Dark	β	SE	β	SE	β	SE	β	SE
<i>Dist. 0 m</i>	0.75*	0.32	1.10*	0.45	2.67***	0.70	1.17.	0.56
<i>Dist. 10 m</i>	0.65**	0.20	0.29	0.41	0.84.	0.49	-0.52	0.52
<i>Dist. 25 m</i>	-0.07	0.30	-0.30	0.43	0.95	0.77	-1.04.	0.55
<i>Dist. 50 m</i>	0.19	0.39	-0.31	0.52	1.35	0.83	0.01	0.64
<i>Dist. 100 m</i>	0.20	0.38	0.30	0.52	2.10	1.62	-1.68.	0.90

‘***’ P < 0.0001; ‘**’ P < 0.001; ‘*’ P < 0.01; ‘.’ P < 0.05

Table 4. Estimates and standard errors per distance step for sites with a turned off streetlight (Off) compared to control dark sites (Dark) after streetlight extinction for the 6 species and 2 genera detected in our study (See Table S5 for the comparison between turned off streetlight sites and full-night lighting sites).

Species	<i>Myotis sp.</i> (n = 3709)		<i>E. serotinus</i> (n = 4544)		<i>N. noctula</i> (n = 648)		<i>N. leisleri</i> (n = 1797)	
	Pseudo-R ²		0.33		0.37		0.15	
Off vs. Dark	β	SE	β	SE	β	SE	β	SE
<i>Dist. 0 m</i>	-1.18**	0.39	1.12*	0.49	2.00***	0.60	2.40*	1.12
<i>Dist. 10 m</i>	-0.94**	0.34	1.50**	0.39	0.53	0.51	1.58.	0.77
<i>Dist. 25 m</i>	-0.58	0.39	0.90.	0.48	0.63	0.53	0.08	0.80
<i>Dist. 50 m</i>	-0.98.	0.38	0.71	0.42	1.72***	0.49	1.57	0.96
<i>Dist. 100 m</i>	-0.16	0.37	-0.08	0.62	0.07	0.70	0.17	1.17

Species	<i>P. pipistrellus</i> (n = 60437)		<i>P. kuhlii</i> (n = 1591)		<i>P. nathusius</i> (n = 720)		<i>Plecotus sp.</i> (n = 516)	
	Pseudo-R ²		0.32		0.23		0.11	
Off vs. Dark	β	SE	β	SE	β	SE	β	SE
<i>Dist. 0 m</i>	-0.59.	0.36	-0.27	0.57	-0.53	0.77	-0.34	0.43
<i>Dist. 10 m</i>	-0.11	0.22	-0.10	0.45	0.14	0.68	-0.44	0.43
<i>Dist. 25 m</i>	-0.43	0.27	-0.50	0.48	0.99	0.82	-1.30*	0.51
<i>Dist. 50 m</i>	-0.45	0.32	-0.78	0.57	2.42**	0.93	-0.55	0.52
<i>Dist. 100 m</i>	0.11	0.29	-0.12	0.64	2.38*	0.93	-0.55	0.54

‘***’ P < 0.0001; ‘**’ P < 0.001; ‘*’ P < 0.01; ‘.’ P < 0.05

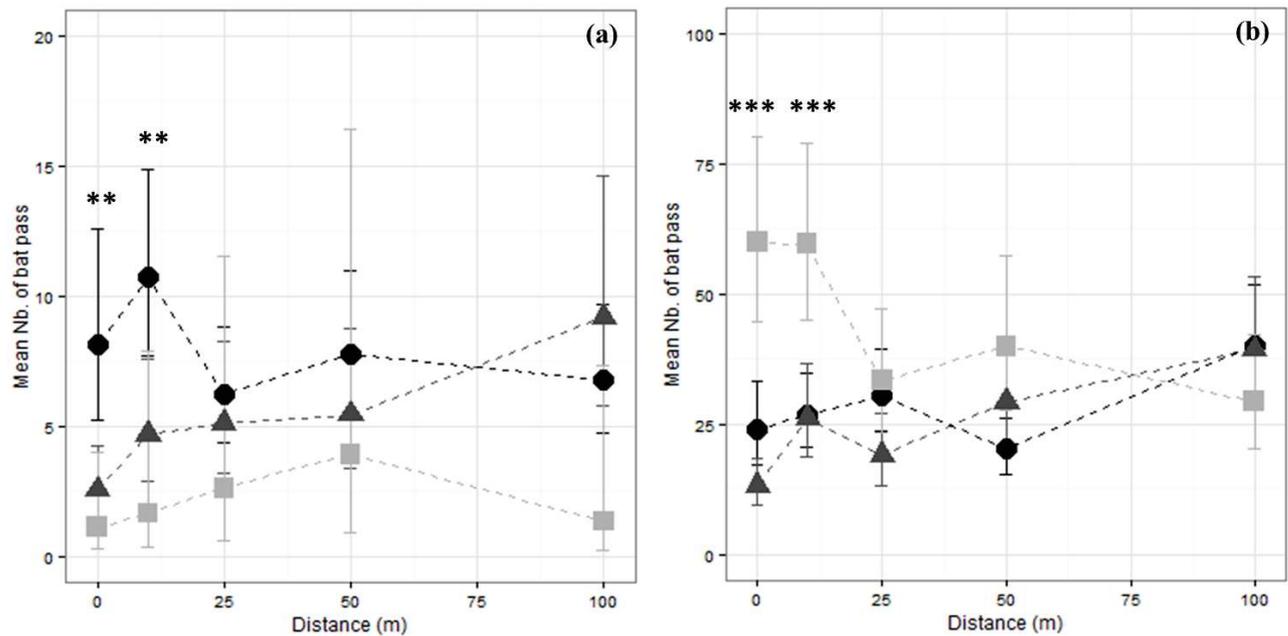


Figure 15. Predicted mean number of bat passes and associated standard errors of (a) *Myotis sp.*, (b) *P. pipistrellus* at each distance step tested on full-night lighting sites (light grey squares), turned off streetlight sites (grey triangles) and on control dark sites (dark dots) after the time of streetlight extinction. Control dark sites (dark dots) for *Myotis sp.* (a) and full-night lighting sites (light grey squares) for *P. pipistrellus* (b) were significantly different from the two other lighting schemes at 0 and 10 meters ('***' $P < 0.0001$; '**' $P < 0.001$).

Effect of light illuminance on bat activity

Vertical illuminance had a significant negative effect on the activity of *Myotis sp.*, even at illuminance values lower than 1 lx ($P < 0.0001$; Figure 16b; Table 5). The activity of *P. kuhlii*, *P. nathusius*, *N. noctula* was the highest at recording stations illuminated by more than 5 lx (Figure 16d; Table 3). However, a peak of activity was observed between 1 and 5 lx for *P. pipistrellus*, *N. leisleri* and *E. serotinus* (Figure 16c; Table 5). For *E. serotinus*, the effect of illuminance even varied across classes, being positive between 1 and 5 lx, and negative below 1 lx and over 5 lx ($P < 0.0001$; Table 5). There was no effect of vertical light illuminance on the activity of *Plecotus sp.*, except at values lower than 1 lx for which the effect was significantly negative ($P < 0.001$; Table 5).

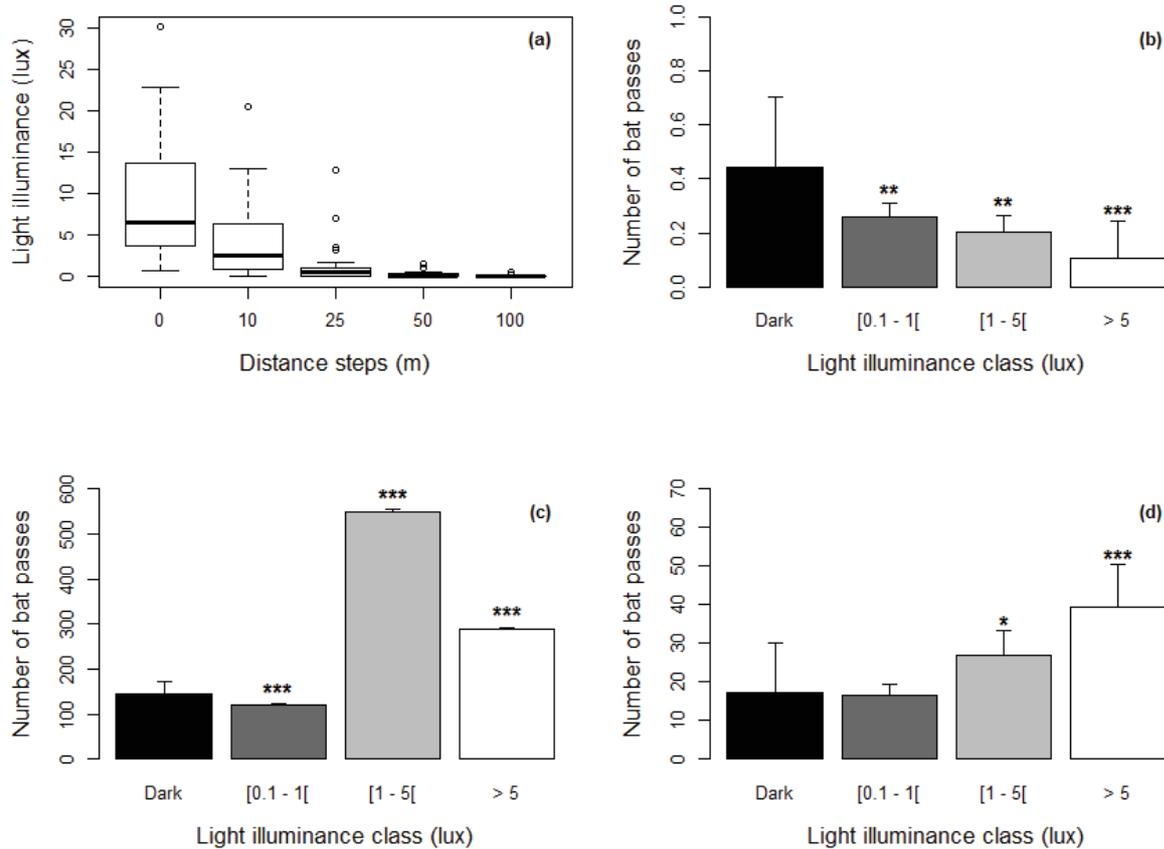


Figure 16. Distribution of vertical light illuminance among the distance steps to the streetlights (a); as well as the predicted mean number of bat pass before the time of streetlight extinction in each light illuminance classes for (b) *Myotis sp.*, (c) *P. pipistrellus*, (d) *P. kuhlii*. The sign ‘*’ indicates that light illuminance classes were significantly different from control dark treatment (‘****’ $P < 0.0001$; ‘***’ $P < 0.001$; ‘**’ $P < 0.01$).

Table 5. Estimates and standard errors for the classes of light illuminance compared to control dark sites (Dark used the intercept) before streetlight extinction for the 6 species and 2 genera detected in our study (‘****’ $P < 0.0001$; ‘***’ $P < 0.001$; ‘*’ $P < 0.01$; ‘.’ $P < 0.05$).

Species	<i>Myotis sp.</i>			<i>E. serotinus</i>		<i>N. noctula</i>		<i>N. leisleri</i>	
Pseudo-R²	0.09			0.24		0.10		0.21	
Int. Dark	<i>n</i>	β	SE	β	SE	β	SE	β	SE
[0.1-1 lx]	81	-0.53**	0.18	-1.15***	0.07	0.63**	0.24	0.02	0.21
] 1-5 lx]	27	-0.77**	0.26	0.39***	0.10	1.29***	0.34	1.82***	0.25
> 5 lx	27	-1.45***	0.32	-0.45***	0.09	1.42***	0.34	1.10***	0.29
Species	<i>P. pipistrellus</i>			<i>P. kuhlii</i>		<i>P. nathusius</i>		<i>Plecotus sp.</i>	
Pseudo-R²	0.22			0.14		0.16		0.09	
Int. Dark	<i>n</i>	β	SE	β	SE	β	SE	β	SE
[0.1-1 lx]	81	-0.17***	0.01	-0.05	0.17	0.57*	0.26	-0.97**	0.36
] 1-5 lx]	27	1.34***	0.01	0.44*	0.22	2.04***	0.30	-0.45	0.46
> 5 lx	27	0.70***	0.01	0.82***	0.25	2.51***	0.29	0.43	0.41

Discussion

Distance of impact of a streetlight on bat activity

Our results revealed that the negative impact of streetlight was detectable between 10 and 25 m away from the streetlight for the light-sensitive *Myotis sp.* and over 50 m for *E. serotinus*. This negative effect remained for *Myotis sp.* even when streetlights were turned off. This highlights that streetlights impact a significant amount of their surrounding habitat and generate additional habitat loss and fragmentation for light-sensitive species, even after streetlight extinction. This is of particular conservation concerns for *Myotis sp.* as this genus is particularly sensitive to habitat loss and fragmentation (Frey-Ehrenbold et al. 2013). Our results were however surprising for *E. serotinus*. Although a negative effect of streetlights was observed at 25 and 50 m, there was no significant difference between lit and dark sites at 0 and 10 m suggesting a light-tolerant behavior at the vicinity of streetlights, and an avoidance behavior at more distant positions. This ambivalent response is consistent with the literature as this species can forage locally at the vicinity of streetlights (Stone et al. 2015a), but it is also negatively affected by artificial lighting at a landscape scale (Azam et al. 2016). Similarly, although *P. pipistrellus* is known to use illuminated areas as foraging patches, its movements and gap-crossing abilities in the landscape can also be altered by artificial lighting (Hale et al. 2015). In this context, our results suggest that as for *P. pipistrellus*, artificial lighting may affect differently the foraging and the transit behaviors of *E. serotinus*. This result would worth further investigations on the fine-scale flight behavior of bats at the vicinity of streetlights to characterize the behavioral shifts that may occur when approaching an artificial light source (Polak et al. 2011).

In contrast, this study confirmed the attraction effect of artificial lighting on the fast-flying aerial hawking species *Pipistrellus sp.* and *Nyctalus sp.* HPS vapor lamps that emit orange

wavelengths are known to be less attractive to insects than broad spectrum white lamps such as high pressure mercury, metal halide or white-LEDs (Blake et al. 1994b; Pawson & Bader 2014). Yet, they still exert a significant “vacuum cleaner” effect that generates a massive accumulation of insect biomass from 0 to 40 m away from streetlights (Perkin et al. 2014a). The pattern of response observed for these 5 species mostly until 10 m (although a 100 m for *N. noctula*), was hence likely a prey-dependent response reflecting aerial insect biomass accumulation under streetlights. Interestingly, the attraction effect of streetlights remained for *N. noctula*, *N. leisleri* and *E. serotinus* once the streetlights were turned off, while it disappeared for the 3 species of *Pipistrellus*. In this context, it would be interesting to investigate the differential effects part-night lighting schemes may have on insect communities in order to get a better understanding of bat prey-dependent responses toward this measure.

Effect of light illuminance on bat activity

Our results also showed a significant negative effect of light illuminance on the light-sensitive *Myotis sp.* even at low illuminance values ranging from 0.1 to 1 lx. The exposure to low light illuminance such as 0.3 lx has also been shown to impact the daily activity and the onset of reproduction of diurnal birds (Dominoni et al. 2013d; de Jong et al. 2016). This suggests that even small changes in natural light regime may have profound impacts on both diurnal and nocturnal biodiversity. However, the vertical illuminance was a better predictor of bat activity than horizontal illuminance. This is not surprising as most bat species use vertical green elements such as hedgerows, forests edges or tree lines to commute between their foraging sites and their roosts in fragmented landscapes (Frey-Ehrenbold et al. 2013). Yet, this suggests that the orientation of the luminous flux and the height of streetlights could be effective parameters to control light trespass on surrounding vertical surfaces.

In contrast, the activity of *P. kuhli*, *P. nathusius* and *N. noctula* increased with light illuminance while the activity of *P. pipistrellus*, *N. leisleri* and *E. serotinus* presented a peak between 1 and 5 lx. The effect of light illuminance below 1 lx and over 5 lx was even negative for *E. serotinus*. This is consistent with the effect of the distance of streetlights as *P. kuhlii*, *P. nathusius* and *N. noctula* presented a peak of activity at 0 m on lit sites (Fig. 1d), whereas a peak of activity on lit sites was recorded at 10 m for *P. pipistrellus*, *N. leisleri* and *E. serotinus* (Figure 10b,c). This shows that fast-flying bat responses to artificial lighting vary according to the level of the light illuminance they are exposed to. Light illuminance is known to increase the predation risk of nocturnal species (Jones & Rydell 1994). Thus, the response of fast-flying bats toward streetlights may be driven by a trade-off between foraging opportunities and predation risk exposure. Overall, our results suggest that the binary classification of light-attracted vs. light-sensitive species may not fully encompass the differential effects artificial lighting may have on a same species.

Management implications

Our results show that the negative effects of streetlight can be detected up to 50 m away from it, and even at light illuminance values as low as 0.1 lx. This highlights the major importance of spatial planning outdoor lighting at large spatial scales to ensure effective protection of dark refuge in human-inhabited landscapes. In 2013, the European commission adopted a “Green Infrastructure Strategy” to promote the development and protection of networks of natural and semi-natural areas in European urban and rural landscapes (EC 2013). However, light pollution issue is absent from the Strategic Environmental Assessment and the Environmental Impact Assessment guidance. Here, we propose distance and illuminance thresholds that may be useful guidelines to identify impacted areas and propose mitigation measures. Additionally, they can be integrated in connectivity modeling approaches to design effective dark ecological corridor networks over large spatial scales. These guidelines are also

relevant for the management of artificial lighting in and around protected areas worldwide, as many are getting surrounded by urban sprawl (McDonald et al. 2009), and more than 30 % of them have already experienced significant increases in nighttime lighting exposure (Gaston et al. 2015).

It is important to note that such guidelines may conflict with security and safety issues especially in and around areas that are used by people during the night. European norm EN13201 for public outdoor lighting recommend to uniformly illuminate pedestrian pathways, and low-traffic roads with a minimum of 7.5 to 10 lx, and commercial areas and access roads with a minimum of 15 to 20 lx (AFE 2007). These thresholds aim at ensuring that i) pedestrians can recognize correctly other people approaching at a given distance and ii) car drivers can identify obstacles and hazards. However, it has been demonstrated that the minimum horizontal illuminance required for pedestrians to detect an obstacle was 0.9 lx (Fotios & Uttley 2016) and that the luminance contrast between obstacles and road background was the best parameter to ensure pedestrian security rather than horizontal illuminance (Tomczuk 2012). This suggests that opportunities exist to dim outdoor lighting at the vicinity of areas of ecological importance without excessive constraints for society. Furthermore, lighting regulations only refer to horizontal illuminance, whereas our study showed that bats were more sensitive to vertical illuminance. Thus, if artificial illumination is locally necessary for security and safety reasons, the limitation of vertical light trespass by adjusting streetlights orientation and height may be effective to limit the negative impacts of outdoor lighting on light-sensitive species.

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Online Appendices

Table S1. Results of the Kruskal-Wallis analysis on whether the surrounding land-uses at the 5 distance steps tested were similar across (a) light treatment (lit/dark) before streetlight extinction and (b) light scheme (dark, turned off, lit) after streetlight extinction. Significant differences were observed between lit and dark sites especially concerning the proportion of impervious surfaces. However, none of these differences resulted in any multicollinearity problems (Variance Inflation Factor (VIF) < 3).

Distance	% forests	% urban	Distance to roads	Distance to water
(a)				
0	X ² = 1.51; P = 0.22	X² = 4.52; P = 0.03	X ² = 3.22; P = 0.07	X ² = 0.10; P = 0.75
10	X ² = 0.36; P = 0.55	X² = 7.48; P = 0.01	X ² = 2.94; P = 0.08	X ² = 0.486; P = 0.49
25	X ² = 1.47; P = 0.23	X² = 14.47; P < 0.001	X ² = 0.36; P = 0.54	X ² = 0.0482; P = 0.83
50	X² = 5.17; P = 0.03	X² = 19.02; P < 0.001	X ² = 3.15; P = 0.07	X ² = 1.33; P = 0.25
100	X² = 4.29; P = 0.04	X² = 17.35; P < 0.001	X ² = 1.37; P = 0.24	X² = 7.34; P = 0.01
(b)				
0	X ² = 1.80; P = 0.41	X ² = 6.17; P = 0.05	X ² = 3.64; P = 0.16	X ² = 0.79; P = 0.67
10	X ² = 1.92; P = 0.38	X ² = 7.83; P = 0.02	X ² = 5.82; P = 0.05	X ² = 0.49; P = 0.78
25	X ² = 2.11; P = 0.35	X² = 14.89; P < 0.001	X ² = 3.81; P = 0.15	X ² = 0.05; P = 0.97
50	X² = 7.09; P = 0.03	X² = 22.58; P < 0.001	X² = 7.23; P = 0.03	X ² = 1.55; P = 0.46
100	X² = 6.06; P = 0.05	X² = 17.39 P < 0.001	X ² = 6.12; P = 0.05	X² = 7.67; P = 0.02

Table S2. Number of bat passes detected for the 6 species and the 2 genera, their % of occurrence (% oc.), as well as the covariables used in final models before and after streetlight extinction, and the response variable distribution (NB = negative binomial; θ = overdispersion coefficient). Statistical models were structured in the following way: $N_{\text{bat passes}} \sim (\text{Light treatment} + \text{covariables}) + (1|\text{municipality/pair})$.

Species	Period	N	% oc.	Covariables	Distribution
<i>P. pipistrellus</i>	Before	35510	93.0	/	Poisson
	After	60437	93.0	Imper. Surf + Open surf. + Roads	Poisson
<i>P. kuhlii</i>	Before	720	38.1	Forest + Open surf. + Roads + Water + T°	NB ($\theta = 4.8$)
	After	1591	38.5	/	NB ($\theta=12.8$)
<i>P. nathusius</i>	Before	210	13.7	/	NB ($\theta = 3.3$)
	After	720	15.2	Forest + Open surf. + Roads + Sunset	NB ($\theta = 2.6$)
<i>E. serotinus</i>	Before	4366	63.0	Open surf. + Imper.surf. + Roads + Water	NB ($\theta = 22$)
	After	4544	42.6	Imper. Surf. + Water	NB ($\theta = 29$)
<i>N. noctula</i>	Before	899	44.4	Open surf. + Roads	NB ($\theta = 10$)
	After	648	22.6	Forest + Imper. Surf. + Open surf. + T°	NB ($\theta=5.8$)
<i>N. leisleri</i>	Before	465	18.9	Forest+ Roads	NB ($\theta = 3.5$)
	After	1797	20.4	Forest + Imper. Surf. + Open surf. + Roads + T°	NB ($\theta=4.8$)
<i>Myotis sp.</i>	Before	2382	42.2	Open surf. + Imper.surf.+ Roads	NB ($\theta = 5.1$)
	After	3709	61.1	Roads + Water	NB ($\theta = 9.8$)
<i>Plecotussp.</i>	Before	482	24.4	Imper.surf. + Water	NB ($\theta = 3$)
	After	516	34.8	Imper. surf. + Roads	NB ($\theta = 5.9$)

Table S3. Increase in the residual deviance of the 2 models before **(a)** and after **(b)** streetlight extinction when removing each explanatory variable one by one calculated with a type II ANOVA with a chi-squared test (***) $\text{Pr}(>\text{Chisq}) < 0.001$, ** $\text{Pr}(>\text{Chisq}) < 0.01$, * $\text{Pr}(>\text{Chisq}) < 0.05$, . $\text{Pr}(>\text{Chisq}) = +/-0.05$).

(a)	<i>P. pipistrellus</i>	<i>P. kuhlii</i>	<i>P. nathusius</i>	<i>E. serotinus</i>	<i>N. noctula</i>	<i>N. leisleri</i>	<i>Myotis sp.</i>	<i>Plecotus sp.</i>
Light treatment	11.27***	0.37	13.39 ***	5.27*	17.96 ***	1.51	6.42 *	0.76
Distance	87.75***	13.96 *	25.78 **	35.59 ***	57.07 ***	55.96***	3.21	9.81 *
Forest	0.97	12.07 ***	0.09	1.06	0.23	25.08 ***	0.77	0.03
Imper. Surf	0.92	1.10	0.00	6.13 *	2.58	1.68	4.96 *	4.24 *
Open surf.	0.8195	11.6855 ***	1.6249	7.1801 **	3.5101 .	0.3455	6.3065 *	0.26
Roads	1.4791	5.52 *	0.40	7.24**	9.50 **	6.38 *	14.31***	0.15
Water	0.0635	7.06**	0.02	10.34 **	0.89	0.10	0.31	4.82 *
Time after sunset	1.26	0.00	0.07	0.00	0.33	2.17	0.00	1.18
Av. Temperature	0.25	4.21 *	0.26	0.77	1.32	1.83	1.22	0.38
Light treatment: Distance	5.81	7.20 *	5.87 .	10.57*	5.83	4.62	8.05 .	12.25 *
(b)	<i>P. pipistrellus</i>	<i>P. kuhlii</i>	<i>P. nathusius</i>	<i>E. serotinus</i>	<i>N. noctula</i>	<i>N. leisleri</i>	<i>Myotis sp.</i>	<i>Plecotus sp.</i>
Light scheme	14.36***	27.93 ***	32.43 ***	28.29 ***	2.30	9.26**	29.68***	3.68
Distance	100.562 ***	33.44 ***	68.88***	63.41***	69.78***	19.26 ***	13.34 **	17.53**
Forest	0.05	20.50 ***	57.73***	0.38	16.85 ***	13.12 ***	0.20	0.00
Imper. Surf	4.44*	0.27	64.47 ***	5.00 *	4.15 *	4.09 *	0.78	8.48 **
Open surf.	5.76 *	0.96	4.89 *	2.18	24.11***	15.30***	1.38	1.50
Roads	5.79 *	0.27	20.63***	0.84	0.94	4.17 *	25.12***	5.31 *
Water	0.69	1.03	0.66	9.14**	0.33	1.60	4.38 *	0.00
Time after sunset	2.40	1.84	12.70 ***	0.45	2.39	0.26	0.00	0.29
Av. Temperature	3.03.	0.01	0.25	2.82 .	23.04 ***	8.91 **	0.29	0.00
Light scheme: Distance	27.09***	13.77.	48.86***	12.05	15.55 *	9.09	7.20	6.97

Table S4. Comparison of AIC between models including as continuous explanatory variables either light illuminance received by a vertical surface (Lux V), light illuminance received by a horizontal surface (Lux H), or the distance (Dist.) from the streetlight (or equivalent dark control). For each species, we used the same set of covariates and the same model structure (as described in Table S2), so that the model with the smallest AIC describes best the observed bat activity before the time of streetlight extinction.

Species	Best Model	AIC <i>lx V</i>	AIC <i>lx H</i>	AIC <i>Dist.</i>	<i>Lx V</i>		<i>Lx H</i>		<i>Distance</i>	
					β	SE	β	SE	β	SE
<i>P. pipistrellus</i>	<i>Lux V</i>	72975	76984	86383	1.15***	0.01	1.01***	0.01	-0.33***	0.01
<i>P. kuhlii</i>	<i>Lux V</i>	1204	1211	1234	1.15***	0.18	0.99***	0.18	-0.34**	0.11
<i>P. nathusius</i>	<i>Lux V</i>	591	605	693	2.28***	0.01	2.18***	0.21	-0.94***	0.17
<i>N. noctula</i>	<i>Lux V</i>	2801	2895	2969	1.34***	0.01	0.98***	0.11	-0.06	0.07
<i>N. leisleri</i>	<i>Lux V</i>	876	909	921	1.60***	0.24	0.92***	0.26	0.08	0.16
<i>E. serotinus</i>	<i>Lux V</i>	4941	4962	4968	0.55***	0.07	0.42***	0.07	-0.23***	0.05
<i>Myotis sp.</i>	<i>Lux H</i>	967	946	983	-0.99***	0.24	-1.88***	0.01	0.15	0.12
<i>Plecotus sp.</i>	<i>Lux V</i>	863	864	917	1.62***	0.20	1.57***	0.19	-0.46**	0.15

‘***’ P < 0.0001; ‘**’ P < 0.001; ‘*’ P < 0.01; ‘.’ P < 0.05

Table S5. Estimates and standard errors per distance step for sites with a turned off streetlight (Off) compared to lit sites (Lit) after the time of streetlight extinction for the 6 species and 2 genera detected in our study.

Species	<i>Myotis sp.</i>		<i>E. serotinus</i>		<i>N. leisleri</i>		<i>N. noctula</i>	
Pseudo-R²	0.33		0.17		0.15		0.37	
Off vs. Lit	β	SE	β	SE	β	SE	β	SE
<i>Dist. 0 m</i>	1.62	1.73	1.75**	0.45	-0.83	0.93	-0.22	0.81
<i>Dist. 10 m</i>	1.54	1.07	2.13***	0.56	-1.42	0.78	0.17	0.70
<i>Dist. 25 m</i>	1.05	1.08	1.48**	0.56	-0.53	0.92	<i>fit. pb</i>	/
<i>Dist. 50 m</i>	1.35	1.22	2.24***	0.59	0.17	1.07	<i>fit. pb</i>	/
<i>Dist. 100 m</i>	2.63	1.46	1.41	0.73	-1.83	1.22	-2.51**	0.8

Species	<i>P. pipistrellus</i>		<i>P. kuhlii</i>		<i>P. nathusius</i>		<i>Plecotus sp.</i>	
Pseudo-R²	0.43		0.32		0.23		0.11	
Off vs. Lit	β	SE	β	SE	β	SE	β	SE
<i>Dist. 0 m</i>	-1.82***	0.41	-3.03***	0.60	-5.76***	1.03	0.96	0.73
<i>Dist. 10 m</i>	-1.26***	0.27	-2.61***	0.53	-4.93***	0.95	0.16	0.64
<i>Dist. 25 m</i>	-0.67	0.37	-2.17***	0.58	-1.36	1.11	-0.83	0.69
<i>Dist. 50 m</i>	-0.24	0.45	-1.23	0.74	-1.56	1.40	1.16	0.98
<i>Dist. 100 m</i>	0.27	0.49	-2.41***	0.74	-3.78***	1.04	-0.27	0.81

fit. pb = Convergence problems in the calculation of the estimates due to the absence of occurrence data of *N. noctula* at the distance steps of 25 and 50 m on full-night lighting sites after the time of streetlight extinction.

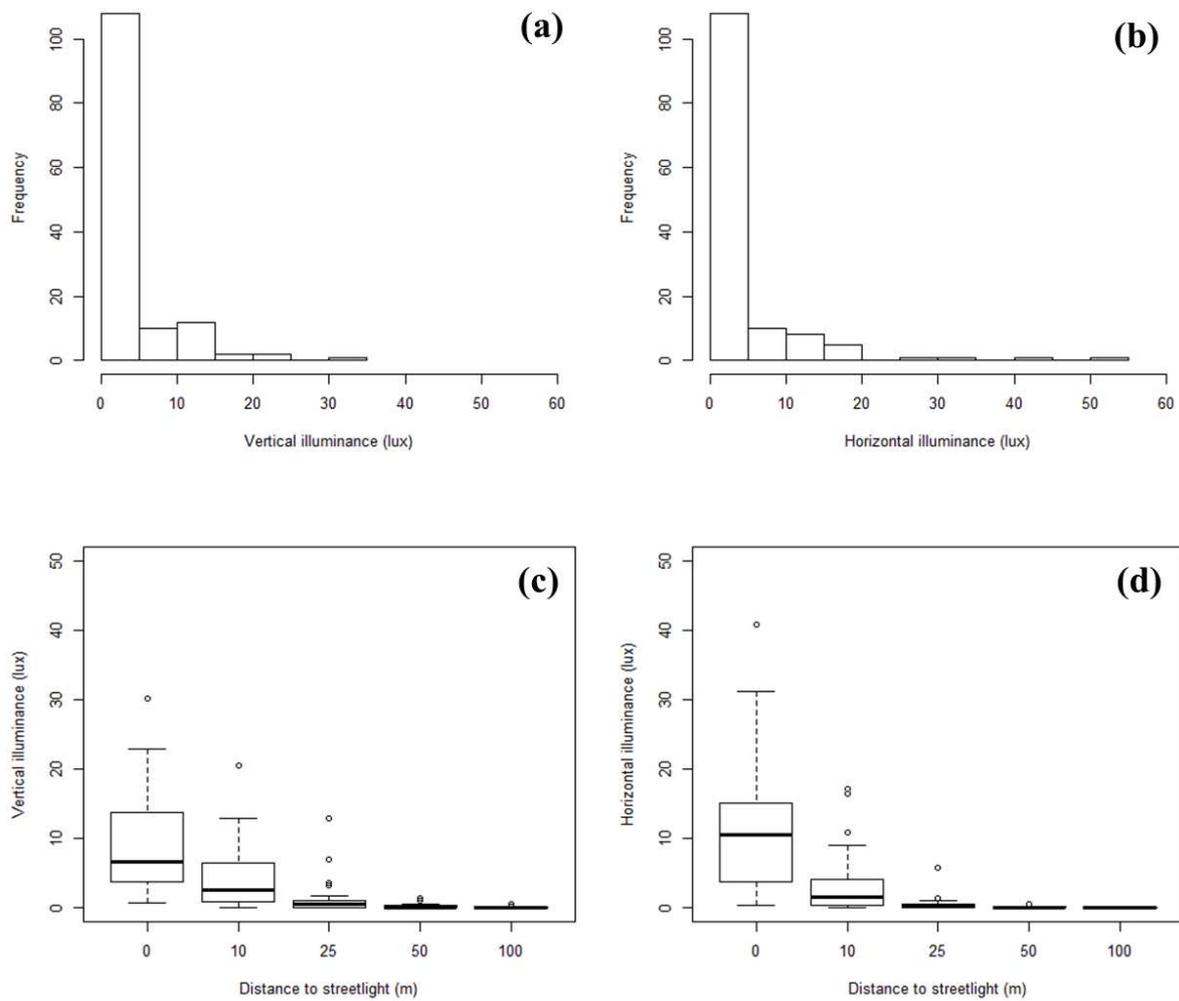


Fig. S1. Histograms and distribution of light illuminance measured vertically (a,c) and horizontally (b,d) across the 5 distance steps where bats were acoustically sampled.

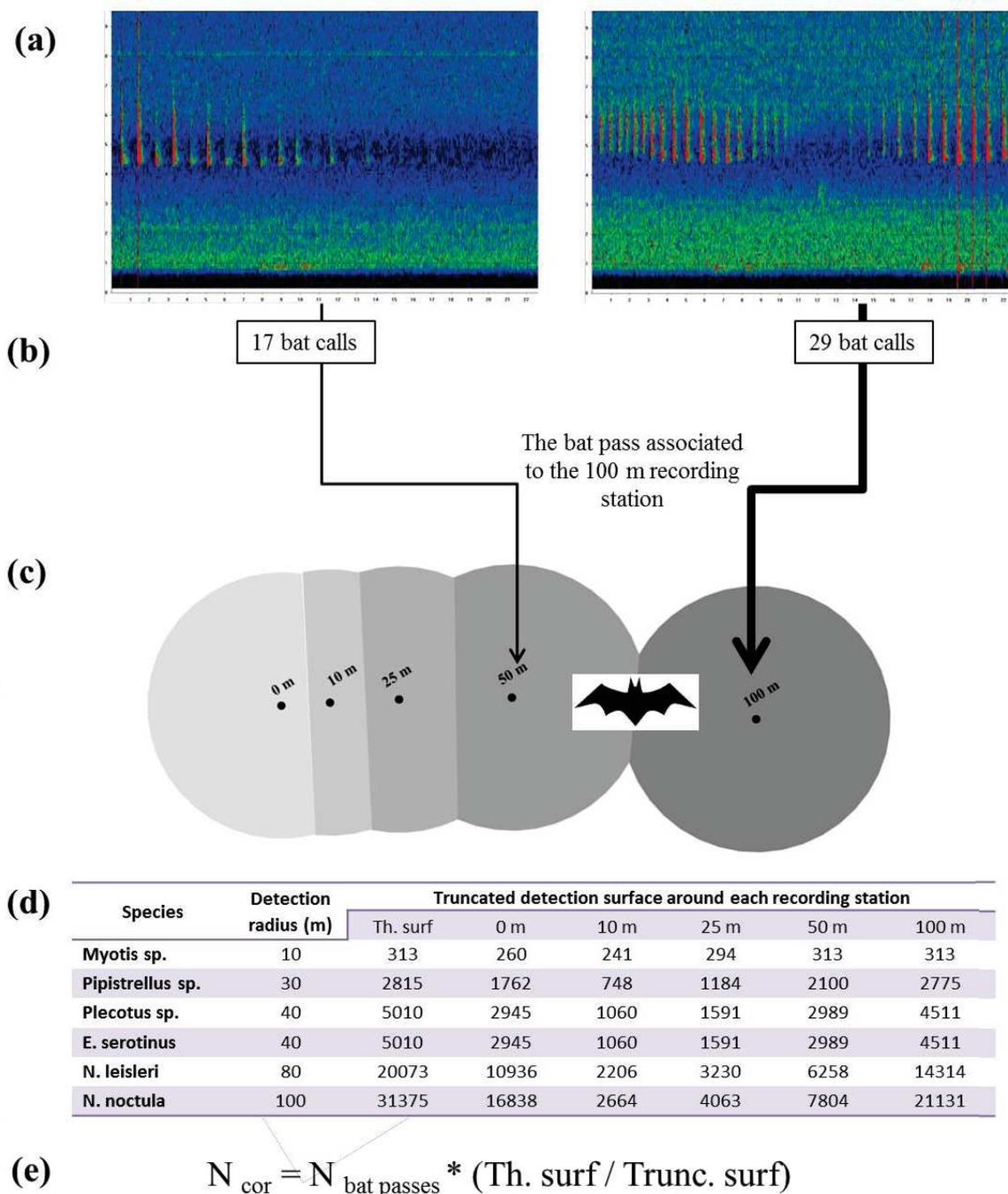


Fig. S2. Correction procedure of the number of bat passes ($N_{\text{bat passes}}$) per recording station with (a) the number of bat passes simultaneously recorded by the recording stations located at 50 and 100 m, (b) the count of the number of bat calls per sequence and the association of the bat pass to one recording station (here at 100 m), (c) the representation of the surface sampled by each recording station (we considered that the species detectability around each microphone was mainly limited to the horizontal plane as the detection radius of all sampled species is inferior to their usual flight height), (d) the theoretical (without overlap) and truncated surface of detection for each species or genera (Barataud 2015) at the 5 recording stations, and (e) the formula used to correct bat activity at the 5 recording stations (N_{cor} was used as the response variable in the analysis).

Discussion & Perspectives

In this experiment, we estimated the distance of impact of streetlights and the threshold of impact of light illuminance on the activity of bats. This study allowed us to elaborate recommendations for the spatial planning of outdoor lighting in human-inhabited landscapes. It revealed that streetlights located up to 50 m away from structural connectivity elements can influence their use by commuting bats. It is however important to note that our experiment was set up along ecotones such as hedgerows and forest edges. The distance of impact of streetlights would likely be different in closed environment such as forests as vegetation stops light propagation. Nevertheless, the distance of impact of streetlights offers valuable information for the management of existing and future ecological corridors. As an example, estimating buffers of impacts around each streetlight in a given landscape would allow i) estimating the proportion of existing ecological corridors that are impacted by artificial lighting, ii) identifying and prioritizing the areas of discontinuity where mitigation measures should be set up (i.e. “barrier effect”), and iii) integrating them in connectivity modeling to calculate landscape matrix resistance to movements.

Concerning this third point, I co-supervised a Master student, Julie Pauwels, with Isabelle Le Viol, Christian Kerbiriou and Aurélie Coulon. She modelled landscape connectivity between urban parks in Paris for *P. pipistrellus*, using acoustic monitoring data from Vigie-Chiro. We used vegetation and built structure characteristics as well as streetlights density to model matrix resistance to movement, and then estimated the likely least-cost paths that could be used by individual bats to move between foraging patches in the city (urban parks). As Julie is now doing her PhD on the integration of light pollution criteria in connectivity modelling, we will try to implement the results from this experiment in the connectivity modeling in Paris,

but also in other French cities that have larger amount of green spaces than Paris (and hence more bat species).

Our results also showed that vertical light illuminance negatively affected the activity of light-sensitive bats even at low values ranging from 0.1 to 1 lux, revealing that low values of illuminance can affect biodiversity. A study on blackbirds also revealed that their reproductive physiology and chronobiology were negatively affected by illuminance values as low as 0.3 lux, which is the average level of lighting urban-living animals are exposed to (Dominoni et al. 2013b, 2013c). This highlights the importance of enhancing the precision of the directionality of streetlights (if they are necessary) to avoid light trespass in the environment. In this context, these illuminance thresholds could be used by lighting professionals to assess if their lighting design effectively mitigates light trespass in areas that are not intended to be lit (Figure 17). However, including these values in connectivity modeling would be complicated as satellite or aerial pictures of nighttime lighting are radiance data which do not describe the amount of light received by a given surface (as illuminance do), but the amount of light emitted or reflected by a given surface (Elvidge et al. 2013). Nevertheless, Bennie et al. (2014b) used the position and height of streetlights as well as high resolution terrain structure data (building and vegetation heights) to model light illuminance propagation in an urban matrix. With such data, it would be possible to use our estimates of illuminance threshold to model landscape connectivity for light-sensitive species. Yet, the authors used airborne light detection and radar (LIDAR) to build their model of light illuminance, which is at the moment an expensive technique that not all administrations can afford.



Figure 17. Example of simulated illuminations of a church in Berlin made by light designers and myself during the light design training school I attended in 2015 (<http://www.cost-lonne.eu/research/light-design-training-school-in-berlin-05-11-10-2015/>). For our simulations, we used the RELUX software (<http://www.relux.biz/>) which is commonly used by light designers. It allows the measurement of light illuminance received by different surfaces and to test different illumination scenarios according to environmental constraints.

Finally, our results tend to show that bat responses to artificial lighting are not only driven by attraction/repulsion behaviors. In particular, so-called “light-attracted” species such as *E. serotinus* showed a contrasted response to artificial lighting, while *P. pipistrellus* activity was highest at intermediate values of light illuminance. This suggests that the response of bats species to artificial lighting is the result of a trade-off between prey intake and predation risk exposure which varies according to the level of illuminance they are exposed to. Furthermore, this trade-off may also differ when they are transiting compared to when they are actively searching for food. This hypothesis is consistent with Hale et al. (2015) who found a negative effect of light illuminance on the gap-crossing behavior of *P. pipistrellus*, and who suggested that artificial lighting affected differently the foraging and the transit activities of this species. Hence, it would be interesting to run fine-scale analysis of bat movements using high-resolution monitoring techniques such as acoustic trajectography or GPS-tracking, to characterize the complex behavioral response of bats toward artificial lighting. These approaches would allow the characterization of flight characteristics such as height, speed and tortuosity, and hence the detection of behavioral shifts when approaching streetlights.

GENERAL DISCUSSION

1. Impacts of light pollution on biodiversity: a multi-scale issue

This PhD is to our knowledge the first study that investigated the impact of light pollution on biodiversity at multiple spatial scales. The results from the chapter 1 revealed the landscape-scale negative effect of artificial lighting on the activity and the probability of occurrence of common fast-flying bat species (often referred as “light-attracted” species). In contrast, consistent with the literature, the results from our experiments showed that these species were locally attracted to streetlights (Rydell & Rydell 1992; Lacoëuilhe et al. 2014). These opposite results can be explained by the fact that the patterns of response (e.g. abundance, distribution) characterized at a landscape scale refer to long-term population dynamics processes, while local-scale studies focus on the behavioral response of individuals (e.g. movements, activity; Fahrig 2003). Hence, our results suggest that even if “light-attracted” fast-flying bats can get foraging advantages from streetlights at a local scale, the amount of artificial lighting infrastructure in the landscape negatively affect their population dynamics. In this context, we can expect an even stronger landscape-scale negative effect of artificial lighting on light-sensitive slow-flying species such as *Myotis sp.* which are known to avoid any source of artificial lighting at a local scale (Kuijper et al. 2008a; Stone et al. 2012; Azam et al. 2015). This raises particular conservation concerns as these species are particularly sensitive to habitat loss and fragmentation (Safi & Kerth 2004). In particular, as light pollution propagates way beyond urban areas (Kyba & Hölker 2013), and is associated to linear infrastructures (e.g. roads), our results suggest that light pollution likely heightens the loss and fragmentation of natural habitats induced by human development. Thus, it appears that research on the large spatial scale effects of light pollution on biodiversity should worth further investigation, especially in the context of the global changes occurring worldwide.

First, it would be interesting to characterize the landscape-scale effects of light pollution on other taxa. Bats are often considered as bioindicators of the response of nocturnal insects to an environmental pressure (Jones et al. 2009). However, the landscape-scale negative effect of light pollution on bats may not only be linked to insect biomass depletion, but also to the negative impacts of artificial lighting on the reproduction success of populations, as well as on landscape connectivity. Thus, it would be interesting to characterize the long-term impacts of light pollution on insect biomass in order to test empirically if similar patterns of response are observed. This is of crucial importance as they are at the basis of most food webs and are key components of ecosystems (Conrad et al. 2006).

Furthermore, it would be worthwhile to examine the large spatial scales impacts of light pollution on diurnal species such as passerine birds which responses may be different to the ones of nocturnal organisms. Light pollution may be less likely to engender habitat loss and fragmentation for diurnal species as they exploit landscape resources during the day. However, it appears to dramatically affect their physiology and chronobiology (Nordt & Klenke 2013; Da Silva et al. 2015b; Dominoni & Partecke 2015). Da Silva et al. (2015a) showed that light pollution was advancing the seasonal onset of dawn and dusk singing of diurnal passerine birds, independently of urban “heat-island” effects. Similar phenological advances were reported for deciduous tree budburst (Ffrench-Constant et al. 2016). Hence, these negative effects on diurnal species temporal dynamics may decrease their reproductive success and survival, which in turn may engender long-term population declines in illuminated landscapes. Furthermore, these impacts may interact and cumulate with the impacts of the increase in temperature induced by climate change (Gaston et al. 2014). This may be of particular importance in temperate regions, as both photoperiod and monthly temperature are crucial environmental parameters that drive species spatial distribution, physiology and seasonal cycles (Bradshaw & Holzapfel 2010; Bennie et al. 2014c). Overall, it

appears that light pollution data should be integrated in macroecological studies that aim at monitoring the impacts of global changes on biodiversity, as it likely interacts and accentuates the adverse impacts of both land-use and climate changes on biodiversity (Gaston et al. 2014).

Finally, light pollution likely have important ecological and evolutionary implications as it may act as a “selective pressure” that drives specific adaptations to illuminated ecological niches for some species and excludes others from illuminated landscapes (Hölker et al. 2010b). As an example, it has been shown that urban populations of small hermine moth *Yponomeuta cagnagella* displayed significantly less flight-to-light behavior compared to rural populations, suggesting that urban environments select individuals that were less attracted to light sources (Altermatt et al. 2016). Large moths (large body mass and wing dimensions) with large eyes tend to be more attracted to artificial light sources (van Langevelde et al. 2011). Hence, light pollution may have selected smaller individuals with smaller eyes, or with different light receptors that change the information processing of perceived light (Altermatt et al. 2016). In this context, characterizing the species life-history traits that are selected or excluded from illuminated landscapes would be crucial to characterize the patterns of changes induced by artificial lighting in biological communities and ecosystem dynamics. The selective pressure light pollution has on microchiropteran bats is unknown. It may select species that have more flexible foraging strategies compared to slow-flying species that are specialized on foraging along or within cluttered vegetation (Safi & Kerth 2004). Furthermore, it may also induce physiological and ecological shifts on populations that can persist in illuminated landscapes. However, it is hard to disentangle so far the selective pressure exerted by artificial lighting relative to other urban components (Shochat et al. 2006). In particular, urbanization is known to drive the replacement specialist urban-sensitive species with more generalist urban-adapted species (McKinney 2006; Devictor et al. 2007; Le

Viol et al. 2012; Deguines et al. 2016). Hence, estimating the influence of light pollution on the biotic homogenization process induced by urbanization would worth further research.

2. Light pollution as an indicator of urbanization process

At a global scale, nighttime sky brightness derived from satellite data has been used as an indicator of local level of economic development as it is highly correlated to local gross domestic product and electric power consumption (rather than population density; Elvidge et al. 1997, 2009b). It has also been integrated in the calculation of global human footprint on natural ecosystems as a proxy of power infrastructure (Sanderson et al. 2002; Venter et al. 2016). However, macroecological studies on the impacts of land-use change on biodiversity have so far mostly used the proportion of built land cover as an indicator of urbanization (Devictor et al. 2007; Penone et al. 2013; Deguines et al. 2016). In the chapter 1, we found that light pollution had a stronger negative effect on bat activity and occurrence than the proportion of impervious surface at a landscape scale. This pattern of response was representative of what likely occurs in mainland France as the proportion of land-covers and radiance used in our analysis was similar to national-scale land covers. These results allowed us to suggest that the ecological impacts of urbanization in France may be underestimated so far by not into account light pollution emissions. Thus, the emergence and accessibility of satellite data of nighttime sky brightness across the world offers great opportunities to elaborate a new indicator of urbanization that would encompass both the proportion of built land covers as well as light pollution emissions. However, it is important to note that these data only describe the radiant flux that is emitted by a given surface (Baugh et al. 2013). They do not account for the sky glow that occurs when artificial lighting is scattered by atmospheric molecules or aerosols and returned to the ground, especially on cloudy nights (Kyba et al. 2011). Although sky glow affects substantial areas around urban and suburban landscapes, its impact on biodiversity dynamics is completely unknown, mostly because of

the difficulty to measure it over large spatial scales (Kyba & Hölker 2013). Hence, the development of sky glow modelling approaches using meteorological and nighttime radiance over large spatial scales would offer valuable additional information for landscape and macroecological studies.

At a regional scale, managing urban growth while minimizing the adverse impacts on ecosystems is becoming a major issue in current and future urban development strategies. Several studies pointed that “compact city scenario” (i.e. relatively small areas with a high density of human settlements separated by large areas of green spaces) was more likely to ensure biodiversity dynamics and ecosystem services for a given human population than “dispersed city scenario” (i.e. low density of human settlements separated by multiple small vegetation remnants; Gagné & Fahrig 2010; Soga et al. 2014; Stott et al. 2015). However, Hale et al. (2013) pointed that high built densities were associated to more extensive, brighter and broader spectrum lighting (high CCT lamps such as LEDs). Simulations of a large-scale replacement of HPS streetlamps by white LEDs (4000 K) over Europe revealed a 2.5 times increase in sky brightness and in landscape-scale light pollution (Kyba et al. 2014b; Falchi et al. 2016). In this context, the ecological benefits of urban densification may be decreased if this process induces an increase in light pollution at a landscape scale. Hence, nighttime artificial lighting data should be included in urbanization scenarios in order to assess what strategy would best cope with social, economic, and ecological goals. This would be particularly crucial for the elaboration of the urbanization strategies of developing countries which are confronted to the emergence of dense megacities with more than 10 million inhabitants, and which are expected to be urbanized further on in the coming decade (Lin & Fuller 2013; United Nations 2014). Thus, the recent development of large-scale nighttime imagery of cities via satellite (VIIRS), astronaut pictures (ISS), or aerial surveys may be of crucial importance in future urban-planning elaborations (Kyba et al. 2014a).

3. Implications for public outdoor lighting planning

Although Europe has experienced an overall increase in sky brightness at a continental scale, some large areas have actually presented decreased sky brightness since the 1990s (Bennie et al. 2014a). Many of these areas correspond to districts with declining industry. However, the authors highlighted that in several regions such as Northern Europe, decreased sky brightness was the result of large-scale modernization of outdoor lighting infrastructure and not economic or industrial decline. Furthermore, landscape-scale simulations of a 10 % reduction in light radiance emissions also revealed a significant increase in the amount of suitable dark patches for biodiversity in Italian protected areas (Marcantonio et al. 2015). These studies suggest that light pollution is a reversible global change, and that it can be limited without excessive costs for human societies.

Current norms for outdoor lighting only take in to account the photometric requirements regarding the visual needs of drivers and pedestrians by defining minimum value of light illuminance that has to be respected for security and safety reasons. European norm EN13201 of 2003 recommend to uniformly illuminate pedestrian pathways, and low-traffic roads with a minimum of 7.5 to 10 lx, and commercial areas and access roads with a minimum of 15 to 20 lx (AFE 2007). However, these recommendations do not take into account the actual outdoor lighting needs corresponding to land-uses and human activities (Kuechly et al. 2012; Hale et al. 2013). It has been demonstrated that the minimum horizontal illuminance required for pedestrians to detect an obstacle was 0.9 lx (Fotios & Uttley 2016). Furthermore, many areas such as offices, commercial and manufacturing areas are already way over the European standards for outdoor lighting (Kuechly et al. 2012; Hale et al. 2013), as lighting norms has not defined maximum levels of light illuminance that should not be exceeded. Thus, Kyba et al. (2014b) have proposed to move beyond lighting norms based on security and energetic standards alone, and to establish “need-based” outdoor lighting planning strategy in order to

illuminate only where and when it is needed. Such approach would be based on a new definition of lighting efficiency in terms of an “efficient provision of lighting” that would simultaneously define the amount of light necessary for a given activity while reducing the environmental impacts of artificial lighting (Kyba et al. 2014b).

In this context, the results of my experiments showed that the most effective way to reduce adverse impacts of light pollution on biodiversity was to limit the spatial extent of lighting especially at the vicinity of natural habitat patches and of ecological corridors. Thus, I propose that vegetation patches, rivers, and structural connectivity elements should be defined in future outdoor lighting planning strategies as specific land-covers where particular artificial lighting management (or absence of lighting) is necessary. In parallel, these recommendations should be built in coherence with the national applications of the European Green Infrastructure Strategy. Our experiment revealed that streetlights should be separated from ecological corridors by at least 50 m to allow their effective use by light-sensitive species and that light trespass on vegetation should be lower than 0.1 lux. Thus, these results could be implemented as a basis of recommendations for outdoor lighting planning at the vicinity of ecological corridors. However, this PhD only focused on bats, and such ecological recommendations require broadening perspectives to multiple taxa. Hence, as a member of the COST “Loss of the Night Network”, I have started with 3 co-authors a systematic review of the scientific literature on the impacts of artificial lighting on biodiversity (See Table 1 for details) in order to extract light spectrum and illuminance thresholds that could be integrated as ecological criteria for future outdoor lighting planning strategies. With this project, we would like to publish a policy paper that would allow assisting stakeholders in the elaboration of new lighting standards and planning methodology.

These recommendations are particularly needed at the moment as we are currently at an important crossroad in outdoor lighting management as most existing lighting infrastructure is

reaching its end-of-life in industrialized countries, and is expanding in developing countries. In the meantime, the increased cost-effectiveness of LEDs which are highly energy-efficient and have good luminous efficacy, will likely engender an exponential deployment of this technology in outdoor lighting in the coming decade (Zissis & Bertoldi 2014). As for many technological innovations, LEDs offer at the same time many opportunities to limit light pollution, but also major risk to increase it (Stanley et al. 2015). On one hand, they can allow light to be directed with unprecedented precision, and dimmed according to human rhythms of activity through the night (Kyba et al. 2014b). They also offer a spectral range that allows adapting light spectrum to different social and ecological contexts. Thus, this technology offers promising options to design outdoor lighting schemes that can limit both the spatial and the temporal extents of lighting at the vicinity of ecological corridors, and restore darkness integrity in human-inhabited landscapes.

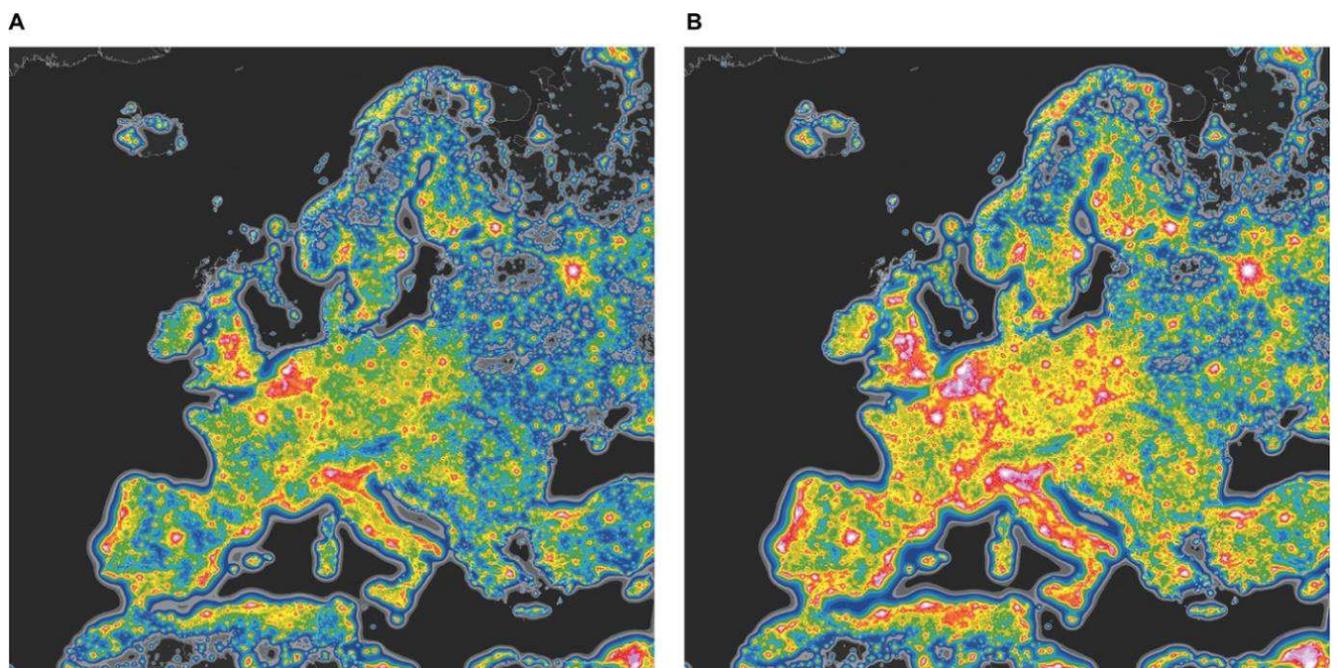


Figure 18. Maps extracted from Falchi et al. (2016) presenting (A) Europe's artificial sky brightness (as a ratio to the natural sky brightness), and (B) a forecast of perceived sky brightness for a dark-adapted eye after a shift toward 4000K CCT LED technology, without increasing the photopic flux of already installed lamps.

However, on the other hand, the deployment of this technology in public infrastructure may come with a “rebound effect” that will impulse an increased use of artificial lighting and an increase in light pollution emissions. This rebound effect has already occurred in the past, following important lighting innovations. Although major improvements in the luminous efficacy of lighting technologies have been implemented in outdoor lighting infrastructures for several decades, worldwide per capita consumption of light remained constant over the years (near 0.7 % of GDP; Kyba et al. 2014a). Concomitantly, the level of light pollution has been increasing every year for several decades in developed countries (Hölker et al. 2010a; Bennie et al. 2014a; Sánchez de Miguel et al. 2014). This reveals that previous lighting technological innovations have actually led to an increase in light pollution emissions through i) the introduction of new artificial light sources in previously unlit areas, and ii) the use of brighter lights sources (Kyba et al. 2014a). Hence, the rebound effect of LEDs is of particular environmental concerns because it will likely increase the spatial extent of lighting in previously unlit areas and the landscape-scale level of light pollution (Figure 18; Falchi et al. 2016). Furthermore, standard white-LEDs present an important peak of energy in the blue range which has major impacts on biodiversity and humans (Schroer & Hölker 2014; Stanley et al. 2015). This important content of blue wavelengths also increases the level of perceived sky brightness in the scotopic band (for dark-adapted eyes; Falchi et al. 2016). In this context, the ongoing shifts in outdoor lighting confirm the crucial importance of elaborating new lighting standards that are not only based on energetic efficiency alone, but also integrate environmental and health concerns (Kyba et al. 2014b). Hence, I intended with this PhD to contribute to the definitions of new ecological criteria that may help limiting the impacts of light pollution on biodiversity.

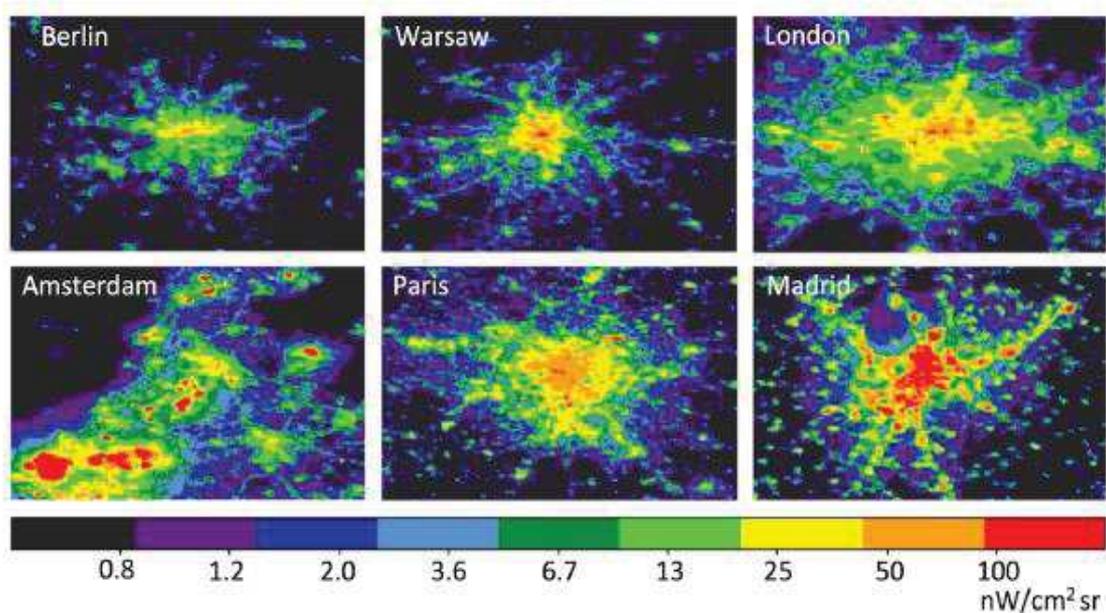


Figure 19. Maps extracted from Kyba et al. (2015) showing the upwelling radiance of six European cities in the VIIRS two-month composite dataset, with a logarithmic color scale (Baugh et al. 2013).

Finally, it is important to note that outdoor lighting planning and light pollution emissions are intrinsically linked to cultural perception of light and darkness, and vary greatly between and within countries (Figure 19; Kyba et al. 2014a). The large scale electric illumination of cities started in the late 19th century in industrialized countries and rapidly became a symbol of modernity, urbanity and security (Meier 2015). It is undeniable that outdoor artificial lighting has provided many benefits for human societies such as safety feeling, increased opportunities for social interactions and liberty of movements in public spaces (Jackle 2001). In this context, it appears of major importance that future outdoor lighting regulations do not consider outdoor lighting planning according to purely operational and technical criteria, but also consider the potentials outdoor lighting offer to society (Meier 2015). Strict compulsory norms for outdoor lighting would likely lead to conflict between planners and users. Hence, characterizing the sociology of use of inhabited areas, as well as including citizens and stakeholders in the decision-making process, will probably be crucial to set up integrated outdoor lighting planning that effectively limits light pollution phenomena while ensuring the social benefits of lighting.

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APPENDIX: Article 4 (from my master project)

Testing the relevance of using spatial modeling to predict foraging habitat suitability around bat maternity: A case study in Mediterranean landscape

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Testing the relevance of using spatial modeling to predict foraging habitat suitability around bat maternity: A case study in Mediterranean landscape



Jocelyn Fonderflick^{a,*}, Clémentine Azam^a, Clarisse Brochier^b, Emmanuel Cosson^c, Delphine Quékenborn^c

^a Centre d'Ecologie Fonctionnelle et Evolutive U.M.R. 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, Montpellier, SupAgro, 1919 route de Mende, 34293 Montpellier, France

^b Syndicat Mixte pour la protection et la gestion de la Camargue Gardoise, Centre de découverte du Scamandre, route des Iscles, Gallician, 30600 Vauvert, France

^c Groupe Chiroptères de Provence, rue Villeneuve, 04230, St. Etienne-les-Orgues, France

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ABSTRACT

Habitat suitability models (HSMs) have so far been used mainly to study broad-scale patterns of species distribution based on environmental variables; however, they can also be applied to address conservation needs at finer scales. In this study, we evaluated the feasibility of using HSMs based on presence-only data to predict bat foraging habitat suitability around maternity roosts using radio-tracking location data. We radio-marked 34 *Rhinolophus ferrumequinum* and 29 *Myotis emarginatus* from two mixed-species maternity roosts (21.5 km apart) in a Mediterranean landscape. We generated foraging habitat suitability maps for the two species and the two colonies incorporating 17 land cover variables as well as distance from the maternity roosts. We then compared the performance of four presence-only models: Mahalanobis distance, ENFA, MADIFA and MaxEnt. Our study found that all four models generated foraging habitat suitability maps that performed well at predicting the species-specific quality of foraging habitat based on the configuration of the landscape. Riparian vegetation, woodland and distance from roosts play a key role in foraging habitat selection around colonies both for *R. ferrumequinum* and *M. emarginatus*. MaxEnt was the model that best predicted suitable foraging habitats. These are also the best models at predicting foraging habitat suitability with relatively good performance around another colony maternity roost using independent radio-tracking locations. Because many bat species are threatened by foraging habitat loss, habitat suitability modeling offers a useful tool in defining appropriate conservation guidelines that protect foraging habitats around bat maternity roosts.

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1. Introduction

During the last decade, habitat suitability models (HSMs), or species distribution models (SDMs), have received considerable attention in conservation studies and have generated a wide range of applications (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). These models have been used both to identify the most influential environmental variables that may explain species occurrence or abundance at known locations and to predict species distribution in relation to biotic and abiotic variables. They have thus enabled a better understanding of species–environment relationships at large spatial scales (Bellamy et al., 2013; Sattler et al., 2007), with the assumption that the probability of the occurrence or abundance of a species is proportional to the degree of habitat suitability (Calenge et al., 2008).

HSMs have also been the subject of significant and rapid methodological development (Elith and Leathwick, 2009). Among the numerous available methods, the widely used generalized linear models (GLMs) are known to provide pertinent results for abundant species (Brotons et al., 2004), but are less reliable for rare species, which produce a high proportion of zero values in the datasets because they are present at only a few locations (Wisz et al., 2008). Moreover, GLMs are based on presence–absence or abundance datasets, whereas many of the datasets available for HSM are presence-only, which raises the issue of choosing “pseudo-absences” to determine whether the species is truly absent or whether it has simply not been observed because of insufficient exploration effort (Hirzel and Le Lay, 2008; Mcardle, 1990).

More recently, several novel HSMs that use presence-only data have been proposed in response to the limitations of models based on presence–absence data: ecological niche factor analysis (ENFA; Hirzel et al., 2002), Mahalanobis distance factor analysis (MADIFA; Calenge et al., 2008) and maximum entropy method (MaxEnt; Phillips et al., 2006). HSMs using presence-only data (e.g. ENFA, MADIFA, MaxEnt) are more suitable for elusive species such as bats, for which local

* Corresponding author at: Centre d'Ecologie Fonctionnelle et Evolutive U.M.R. 5175, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, Montpellier, SupAgro, 9 rue Celestin Freinet, 48400 Florac, France.

E-mail address: jocelyn.fonderflick@supagro.fr (J. Fonderflick).

absence data are often not available or reliable because of their low detectability due to their nocturnal behavior, the difficulties of acoustic identification (Ahlén and Baagøe, 1999; Barclay, 1999) and their high mobility (Jaberg and Guisan, 2001; Walsh and Harris, 1996). HSMs in bat studies have mostly been developed with the primary goal of predicting species distribution in relation to environmental variables, especially climatic variables, at a large spatial scale (see e.g. Greaves et al., 2006; Rebelo and Jones, 2010; Sattler et al., 2007). However, HSMs may also offer opportunities for predicting habitat suitability at finer scales, for instance, in relation to landscape configuration (see e.g. Razgour et al., 2011). However, characterizing or predicting habitat suitability at a fine spatial scale in relation to landscape configuration can be more problematic for mobile species than for sessile species, as the former tend to use intermittent resources that are patchily distributed across a landscape (Elith and Leathwick, 2009). To date only one study (Razgour et al., 2011) has explored the feasibility of predicting bat foraging habitat suitability at a fine spatial scale using HSM based on presence-only data. The satisfactory results obtained for the gray long-eared bat *Plecotus austriacus* in the UK (Razgour et al., 2011) need to be tested for other bat species in different contexts.

Many bat species around the world are increasingly threatened by anthropogenic land-use intensification (Mickleburgh et al., 2002) which affects both their access to foraging habitat and their ability to establish colonies: two key elements for the conservation (Fenton, 1997). Because the majority of bat species form colonies, they are vulnerable to local disturbance. Bat conservation efforts mainly focus on hibernacula or maternity roosts and rarely on the foraging habitat surrounding maternity roosts. Despite the significant development of telemetry studies on bats in recent years, the characterization of favorable foraging habitat surrounding maternity roosts and its explicit spatialization using predictive models – both of which are needed to plan effective conservation management actions for habitats – remain very limited (see however Rainho and Palmeirim, 2013). In this context, HSM could be used to generate foraging habitat suitability maps surrounding maternity roosts that allow the species-specific quality of the foraging habitat to be predicted based on the landscape configuration of the study area (Rainho and Palmeirim, 2013; Razgour et al., 2011). These models could be useful tools to help identify where and how species use foraging habitats.

Indeed, by helping conservation management staff to better identify key foraging habitats, HSMs could be used to define appropriate conservation guidelines for protecting foraging habitats around maternity roosts of threatened species.

The aim of this study was to evaluate the relevance of HSM based on presence-only data to predict bat foraging habitat suitability around maternity roosts using as a biological model two different bat species of conservation concern, the greater horseshoe bat *Rhinolophus ferrumequinum* and Geoffroy's bat *Myotis emarginatus*. More specifically, we compared the performance of four different presence-only models (Mahalanobis distance or MD, ENFA, MADIFA and MaxEnt) using radio-tracking location datasets of these two species within the foraging areas of two mixed-species maternity colonies in the French Mediterranean area. Our objectives were: (1) to characterize the selection of foraging habitat of the two bat species at a fine spatial scale; (2) to assess the relative performance of the four presence-only models in creating suitability maps for foraging habitat around the two colonies; and (3) to assess the performance of these models at predicting foraging habitat suitability around another independent bat colony.

2. Materials and methods

2.1. Study area

Our study site was located in the Camargue (the delta of the Rhône River) on the French Mediterranean coast (43° 34' N, 4° 34' E; Fig. 1). The climate is typically Mediterranean, with warm average daily temperatures (3–11 °C in January, 19–30 °C in August) and low rainfall (590 mm year⁻¹ on average) (Chauvelon, 1998). Northerly and north-westerly winds are very common throughout the year, and there is significant evapotranspiration (1300 mm year⁻¹) (Chauvelon, 1998). The Camargue is characterized by flat landscapes with soil containing an increasing gradient of salt as it approaches the Mediterranean Sea. The area consists mainly of lagoons and a marshy network with some salt grasslands. Forest areas are small and dominated by *Populus alba* (L.) and *Pinus pinea* (L.). The drainage system of the Camargue is entirely controlled by man-made dykes located where marine and river water

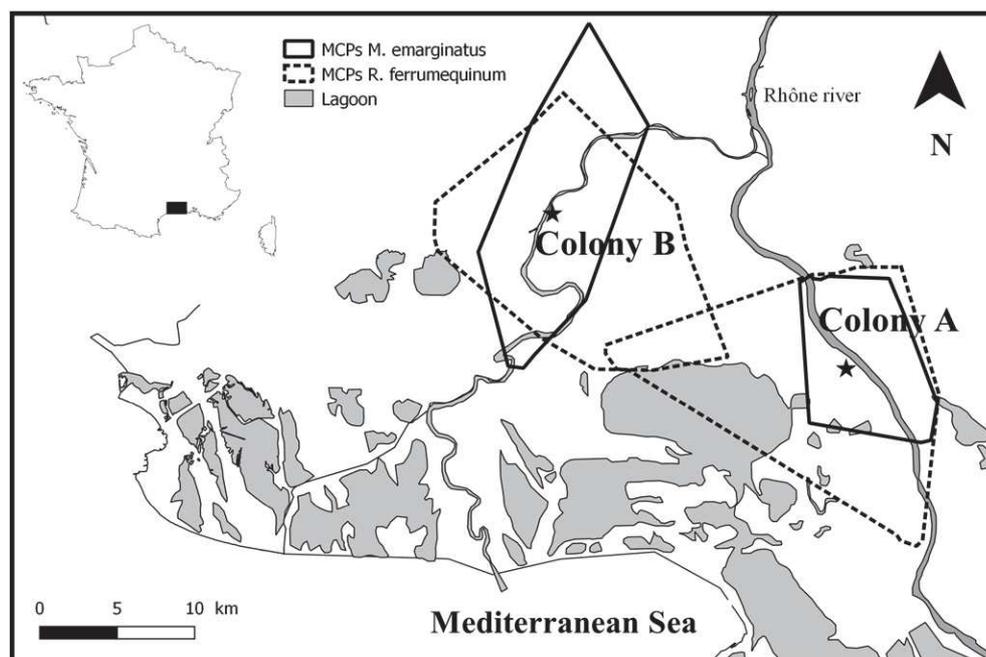


Fig. 1. Location of the study area with the four minimum convex polygons (MCPs) for *Rhinolophus ferrumequinum* and *Myotis emarginatus* around the two mixed-species maternity roosts (colonies A and B indicated by a star).

enters the delta. These dykes have allowed the establishment of agriculture dominated by cereal crops (mainly rice and wheat) and the development of extensive horse and cattle ranching.

2.2. Radio-tracking data

We radio-marked a total of 34 *R. ferrumequinum* (25 adults and 9 juveniles) and 29 *M. emarginatus* (24 adults and 5 juveniles) from two mixed-species maternity roosts at a distance of 21.5 km from each other (Table 1). In one monitored colony (colony A), the individuals were marked in 2010 and included 14 *R. ferrumequinum* and 13 *M. emarginatus*; in the second colony (colony B), the individuals were marked in 2011 and included 20 *R. ferrumequinum* and 16 *M. emarginatus*. Individuals were captured using mist nets placed near the colony early in the night. Both bat capture and handling were carried out with the authorization of local nature conservation authorities. Captured individuals were weighed and then equipped with a radio transmitter (LT5 or LT6, Titley Scientific UK) attached to the bat's interscapular region with Skinbond surgical adhesive. The weight of the attached transmitter, ranging from 0.35 to 0.70 g, represented less than 5% of each bat's weight so as not to affect its movement (Aldridge and Brigham, 1988). Individual bats of both species were monitored over two two-week field sessions: the first session before parturition (colony A: 13 nights from 9 to 22 June; colony B: 13 nights from 10 to 23 June) and the second after parturition (colony A: 17 nights from 23 July to 9 August; colony B: 17 nights from 16 July to 2 August). Each individual bat was monitored for several consecutive nights by five different teams in cars positioned in the field. The teams were equipped with radio receivers (Australis 26k™ Scanning Receiver, Titley Scientific UK) with a three or four-element Yagi antenna. Between two and four bats were tracked each night for as long as the radio transmitter batteries functioned. The bats' locations were recorded in five-minute intervals over the entire night by biangulating or triangulating the signal direction and then treating the data with LOAS 4.0 (Ecological Software Solutions LLC). This software uses "best biangulation" and "maximum likelihood estimator" to estimate locations using bi- or triangulation. We then used ArcGIS 10 to plot a minimum convex polygon (MCP, White and Garrott, 1990) for each species and each colony (Fig. 1). We subtracted the entire area of lagoon on the MCP for *R. ferrumequinum* in colony A for the statistical analysis of foraging habitat selection and habitat suitability (section "Habitat suitability modeling") because no bat locations were obtained for this habitat. We interpreted signal features to assess bat activity: large-scale, rapid movements between two consecutive locations represented commuting, whereas slower movements in a restricted area between two consecutive locations suggested foraging. Locations of commuting bats were excluded from the statistical analysis.

2.3. Environmental data

We initially selected 20 eco-geographical variables (EGVs) which satisfy one of three main criteria: they have a large surface area in the study area (e.g. arable land, old and new wasteland, salt marsh and wetland); they are important for the distribution of bat species in general

(e.g. hedgerow, isolated tree, riparian vegetation); or they are important predictors of the specific foraging habitats of *R. ferrumequinum* and *M. emarginatus* (e.g. perennial crop, semi-open grassland, woodland; Roué and Barataud, 1999). These EGVs were mapped into the SIG Arcgis 10 software (Esri, France 2012) using aerial photographs from 2010 and 2011 with a resolution of 15–20 cm.

The four MCPs were divided into square cells of 1 ha (100 m × 100 m), consistent with the precision of the EGVs maps and of the bats' locations. For 18 EGVs, we used GIS to calculate the distance between the center of each cell and the nearest relevant EGV. We assessed the landscape context within a 300-m buffer around MCPs to take into account outlying environmental variables on the MCPs (Powell, 2000). For the last two EGVs (isolated tree and hedgerow), we calculated the number of isolated trees and the length of hedgerows within a 150-m circular radius around the center of each cell. Our quantitative EGVs, based on datasets that included distance variables between each cell and the nearest EGV, take into account the landscape context around cells (Rainho and Palmeirim, 2011).

The distance values of all EGVs were transformed into square roots to improve normalization before analysis. We checked multicollinearity among the 20 EGVs for each MCP. We found a positive Pearson correlation (with $r > 0.70$) between the EGVs woodland and forest edge adjacent to open space and river and riparian vegetation for three of the four MCPs. We thus removed forest edge adjacent to open space and river EGVs for HSMs. Statistical analysis is thus based on 18 EGVs (Table 2).

2.4. Statistical analysis

2.4.1. Spatial autocorrelation

To minimize potential problems related to the spatio-temporal non-independence of radio-tracking locations (Swihart and Slade, 1985), we used Moran's *I* correlograms built for the 18 EGVs selected. We randomly distributed 1000 points on each of the four MCPs and calculated the distance to each point from the nearest relevant EGV using GIS. Moran's *I* correlograms were built for each EGV with 11 lags of 2 km each for the two MCPs for *R. ferrumequinum*, and six lags for the two MCPs for *M. emarginatus*. We assessed the significance of the values for each lag with a Monte-Carlo test of 999 permutations. A correlogram was significant if at least one lag resulted in $p < 0.05$. Few significant spatial autocorrelations were found for the 18 EGVs selected beyond 6 km for *R. ferrumequinum* and beyond 4 km for *M. emarginatus*, and those significant values corresponded to small autocorrelation (Moran's *I* < 0.20). Based on the flight speeds of other similar species (Polack et al., 2011), we assumed that in direct flight *R. ferrumequinum* and *M. emarginatus* travel 4 to 6 km in 10 min, a flight speed from 25 to 35 km/h. Thus, for the purposes of our statistical analysis, we retained only locations that were at least 10 min apart. However, to avoid pseudo-replication we removed duplicate localizations resulting from overlapping core foraging habitat between bats or several locations measured for the same bat at the same area (Razgour et al., 2011); we did this by using only one location record per 1-ha cell. In the steps to avoid pseudo-replication, more than half of the measured locations were excluded before the statistical analysis (Table 1).

Table 1

Description of radio-tracking locations for *Rhinolophus ferrumequinum* and *Myotis emarginatus* obtained at two mixed-species maternity roosts (colonies A and B) with N: the number of individuals surveyed for each species; mean distance: the mean distance between the colony and the foraging habitat; maximum distance: the maximum distance between the colony and the foraging habitat; MCP area: minimum convex polygon area calculated with all locations.

Species	Colony	N	Mean distance (km)	Maximum distance (km)	MCP area (km ²)	Number of locations			
						Total	Selected for analysis	Train data	Test data
<i>R. ferrumequinum</i>	A	14	5.0	15.6	207.5	624	277	194	83
	B	20	3.0	14.9	196.9	1449	522	366	156
<i>M. emarginatus</i>	A	13	3.8	14.4	74.1	250	104	73	31
	B	16	4.3	12.6	129	697	273	192	81

Table 2

Description of the 18 eco-geographical variables (EGVs) used in the Habitat Suitability Models (HSMs) for *Rhinolophus ferrumequinum* and *Myotis emarginatus* on the two mixed-species maternity roosts.

Variable category	Description
Isolated tree	Number of isolated trees (over 7.5 m in height) within a 150-m circular radius around the center of each cell
Sparse woodland	Distance of each cell to the nearest mixed deciduous and conifer forest with a width >20 m and a ground cover between 50 and 90%
Dense woodland	Distance of each cell to the nearest deciduous forest with a width >20 m and a ground cover >90%
Perennial crops	Distance of each cell to the nearest perennial crops (vines or fruit trees)
Colony	Distance of each cell to the maternity roost
Old wasteland	Distance of each cell to the nearest agricultural land abandoned for >5 years and <30 years
New wasteland	Distance of each cell to the nearest agricultural land abandoned for <5 years
Arable land	Distance of each cell to the nearest paddy fields, gardened area or cereal fields
Hedgerow	Length of hedgerow within a 150-m circular radius around the center of each cell
Park	Distance of each cell to the nearest park or garden
Open grassland	Distance of each cell to the nearest grassland with <10% shrub cover
Semi-open grassland	Distance of each cell to the nearest grassland with shrub and tree cover between 10 and 50%
Salt grassland	Distance of each cell to the nearest salty area associated with halophytic herbaceous vegetation
Riparian vegetation	Distance of each cell to the nearest riparian vegetation
Road	Distance of each cell to the nearest highway or national or local road
Salt marsh	Distance of each cell to the nearest salty area associated with halophytic vegetation type <i>Salicornia</i>
Village	Distance of each cell to the nearest urbanized area >4 ha
Wetland	Distance of each cell to the nearest large area of open water associated with plant communities dominated by reeds

2.4.2. Habitat suitability modeling

We compared four different HSMs based on presence-only data to assess their performance to predict bat foraging habitat suitability around maternity roosts: Mahalanobis distance (MD, Clark et al., 1993), ENFA, MADIFA and MaxEnt. The last three HSMs were developed quite recently. MD, although an older method, is considered powerful enough to predict habitat suitability (Tessarolo et al., 2014; Tsoar et al., 2007).

We used MaxEnt and ENFA models to characterize the foraging habitat selection of the two species and the two colonies. MaxEnt estimates an index of habitat suitability based on the probability distribution of maximum entropy (i.e. the distribution that is most spread out, or closest to uniform), subject to a set of constraints that represent incomplete information about the target distribution (Phillips et al., 2006). ENFA was used to compare the cell values where a bat species occurred with cell values in the MCP from the 18 EGVs. The ENFA summarized all EGVs into a few uncorrelated mutually orthogonal factorial axes (i.e. those explaining the largest part of the variance), in a similar way to principal component analysis (Basille et al., 2008; Hirzel et al., 2002). The first factorial axis of the ENFA, named marginality, maximizes the multivariate distance of the 18 EGVs between the cells occupied by the species and all the cells within the whole reference area (i.e. within the MCP). The other factors, named specialization, maximize the ratio between the variance of all the cells in the MCP with the variance of the cells in which the bat species occurred.

For the ENFA, we first performed a Monte Carlo test based on 999 permutations to determine whether the foraging habitat selection of the two bat species and the two colonies was significantly different from all EGVs in the MCPs (Hirzel et al., 2002). We also calculated the correlation coefficient between the 18 EGVs selected and the marginality factors, which are often the most biologically important for interpretation (Calenge et al., 2008). This step allowed us to determine which variables were relevant to explain foraging habitat selection around the two colonies. The higher the absolute value of this coefficient, the more the EGV explained bat foraging habitat selection. With distance variables, negative coefficients indicated that bat species preferentially select this EGV, and positive coefficients indicated a negative association with this EGV. The MaxEnt model provided the percentage of an environmental variable's contribution to habitat suitability. Similar to the ENFA, the higher the percentage, the more the EGV explained bat foraging habitat selection.

In the first step, we created foraging habitat suitability maps around the two colonies and for the two bat species with the 18 EGVs using four HSMs: Mahalanobis distance (MD), ENFA, MADIFA and MaxEnt. These HSMs assume that the probability of occurrence of a species is

proportional to the level of habitat suitability (Calenge et al., 2008). We ran 20 replicates of each HSMs for each species and each colony. In each replicate, the foraging habitat suitability maps of the four MCPs from each HSMs were built using 70% of the available presence data, randomly selected (train data); the remaining 30% (test data) were used to test the predictive performance of models (Table 1). MaxEnt models were ran using the default MaxEnt settings with 500 iterations. We tested for any effect of modifying the regularization betamultiplier value on model complexity and reducing overparameterization by running models with regularization betamultiplier values equal to 1, 2 and 3. We used the software ENMtools (version 1.4.3; Warren et al., 2010) to select the most parsimonious, best fit model based on corrected Akaike's information criterion (AIC_c) scores (Warren and Seifert, 2011). Following Merow et al. (2013), we used raw output for produce foraging habitat suitability maps.

In the second step, we also tested whether or not the model calibrated on one colony was able to accurately predict the habitat suitability of the second colony. We used all EGVs in a first analysis and the most important EGVs in terms of habitat selection in a second time. We used the results of the jackknife test of MaxEnt models using area under curve (AUC) on test data for each EGV individually in order to find most important EGVs for transferability (Phillips, 2008). We use AUC_{test} rather than regularized gain to determine the performance of different variables because our goal is to assess the performance of HSMs at predicting foraging habitat suitability around other bat colonies based on AUC evaluation. In the first step, we listed all EGVs with an AUC_{test} alone >0.60 for *R. ferrumequinum* and *M. emarginatus*. In the second step, we selected the combination of EGVs that maximize the AUC evaluation. HSMs of each species were built from all locations of one of the two colonies (train data), and then all locations of the second colony (test data) were used to test the predictive performance of the models. In the last analysis, we tested if the MaxEnt models differ significantly from what would be expected by chance by comparing the significance of the AUC value of the MaxEnt models derived from the most important EGVs with the AUC values obtained from a null-model (Raes and ter Steege, 2007). Null-models were generated by randomly selecting a number of points equal to those in the test data of each species in each MCP, and repeated 99 times to generate a frequency histogram of AUC values. The AUC of MaxEnt model was then compared with the 99% confidence interval of the 99 AUC values obtained with a null-model.

2.4.3. Model evaluation

HSMs were evaluated using two presence-only statistical measures. We chose these two statistics because they each quantify different

aspects of model performance: AUC of the receiver operating characteristic (ROC) and the Pearson's correlation coefficient (COR, Elith et al., 2006). AUC is the most-used statistic in HSM studies. Model performance is deemed low when AUC values are between 0.50 and 0.70, good when $AUC > 0.70$, and very good when greater than 0.90 (Baldwin, 2009). COR is known as the "point biserial correlation" and can be calculated as a Pearson correlation coefficient between the test data and the prediction (Elith et al., 2006).

Except for the MaxEnt model, all the statistical analyses were performed using R 2.14.1 software (R Development CoreTeam 2013). More specifically, we used the packages "adehabitat" (Calenge, 2006) "pROC" (Robin et al., 2011) and "dismo" (Hijmans et al., 2015). The MaxEnt model was fitted with maximum entropy species distribution modeling, version 3.3.3e (Phillips et al., 2006).

3. Results

3.1. Patterns of foraging habitat selection

The areas of the respective MCPs for *R. ferrumequinum* and *M. emarginatus* calculated using all the locations collected during the two field sessions were 207.5 km² and 74.1 km² for colony A, and 196.9 km² and 129 km² for colony B (Table 1, Fig. 1). For both species, bats generally return to the same colony after each night. The foraging habitat locations were on average between 3 and 5 km from the colony (Table 1), with 73.5% of locations within 5 km for *R. ferrumequinum* and 54.2% for *M. emarginatus*. The foraging habitat of *R. ferrumequinum* was significantly more distant than that of *M. emarginatus* for colony A (Kolmogorov–Smirnov test, $p < 0.01$), and the inverse was true for colony B (Kolmogorov–Smirnov test, $p < 0.001$). The foraging locations most distant from colonies were found at 15.6 km for *R. ferrumequinum* and 14.4 km for *M. emarginatus* (Table 1).

The Monte-Carlo test between the mean value of cells used by the two bat species in the two colonies and the mean value of the cells in each MCP was highly significant ($p < 0.001$) for the marginality factor of ENFA. For the first specialization factor of the ENFA, it was only significant ($p < 0.01$) for the two species in colony B, for the 18 EGVs used. The Monte-Carlo test showed that the two species use very restrictive foraging habitats that significantly differ from the average habitat found in each MCP. The EGVs explaining foraging habitat selection present some similitude between the two colonies and the two species.

For example, neither of the two species use lagoons as a hunting habitat. Both ENFA and MaxEnt results show that riparian vegetation, woodlands (dense or sparse) and distance from the maternity roost play a key role in foraging habitat selection around a colony both for *R. ferrumequinum* and *M. emarginatus* (Table 3). These four EGVs together contributed to the overall MaxEnt model performance by 37.1% (colony A) and 62.7% (colony B) for *R. ferrumequinum*, and 49.2% (colony A) and 45.8% (colony B) for *M. emarginatus* (Table 3). The patterns of foraging habitat selection presented some differences between the two species and between the two colonies. The locations of *M. emarginatus* are significantly closer to semi-open grassland in colony B than in colony A (Kolmogorov–Smirnov test, $p < 0.001$), i.e. semi-open grassland areas are more often selected as foraging habitat by individuals of colony B than of colony A. Wetlands are significantly more negatively associated in colony A than in colony B for the two species (Kolmogorov–Smirnov test, $p < 0.001$ for *R. ferrumequinum* and *M. emarginatus*). Dense woodland is more selected by *R. ferrumequinum* in colony A than in colony B (Kolmogorov–Smirnov test, $p < 0.001$) and sparse woodland in colony B than in colony A (Kolmogorov–Smirnov test, $p < 0.001$). Finally, the length of hedgerows and the number of isolated trees do not appear to play any special role in the foraging habitat selection of either species in either colony.

3.2. Prediction of foraging habitat suitability map

All four presence-only models used for mapping foraging habitat suitability of the two species and the two colonies had good predictive performance (all $AUC_{test} > 0.74$; Fig. 2). The most parsimonious MaxEnt models based on AIC_c scores for the two bat species in the two colonies involved the regularization betamultiplier values equal to 3. There was a strong significant positive correlation between the score of AUC_{test} and COR ($r = 0.69$, $N = 16$, $p < 0.01$) calculated for the four models for the two species and the two colonies.

The MaxEnt models performed better when compared with MD, ENFA and MADIFA on the basis of the two predictive performance measures used, i.e. AUC_{test} and COR (Fig. 2). The predictive performance of MaxEnt models ($AUC_{test} > 0.82$) was good to very good for mapping foraging habitat suitability around the two colonies for both species (Fig. 3). However, the predictive performance of foraging habitat suitability around colony B from the model fitted on colony A (and inversely colony A on B) was low (all $AUC_{test} < 0.67$) when the 18 EGVs were used

Table 3
Contribution of the 18 eco-geographical variables (EGVs) used in modeling foraging habitat suitability for *Rhinolophus ferrumequinum* and *Myotis emarginatus* around the two mixed-species maternity roosts (colonies A and B) according to MaxEnt and ENFA models. For MaxEnt, the model gives the percentage of variance explained by each EGV, and for ENFA, the model gives the correlation between the 18 EGVs and the marginality factors (Mar.). With distance measures, negative coefficients indicate that bat species preferentially select this EGV, and positive coefficients indicate that bat species are not associated with this EGV. Values ≥ 9 for MaxEnt and $\geq \pm 0.30$ for ENFA are in bold for an easier visualization of the table.

Eco-geographical variables	<i>R. ferrumequinum</i>				<i>M. emarginatus</i>			
	Colony A		Colony B		Colony A		Colony B	
	MaxEnt	Mar.	MaxEnt	Mar.	MaxEnt	Mar.	MaxEnt	Mar.
Isolated tree	2.40	-0.06	0.40	0.08	0.20	-0.10	2.20	0.03
Sparse woodland	2.70	-0.02	14.70	-0.35	0.30	-0.09	2.10	-0.20
Dense woodland	13.20	-0.49	1.90	-0.34	14.40	-0.45	9.50	-0.46
Perennial crops	2.70	-0.07	1.70	-0.22	2.00	-0.14	5.00	-0.19
Colony	6.40	-0.26	28.50	-0.49	8.40	0.04	19.20	-0.33
Old wasteland	8.50	0.36	1.00	0.08	2.00	0.13	6.30	0.17
New wasteland	0.70	0.02	2.30	-0.17	0.20	0.09	1.70	0.13
Arable land	4.90	0.16	1.50	-0.11	2.10	0.15	1.60	0.09
Hedgerow	1.90	-0.12	2.20	0.20	2.90	0.13	2.10	0.20
Park	2.80	0.16	2.10	-0.03	3.10	-0.25	4.10	-0.01
Open grassland	4.00	-0.15	0.60	-0.06	0.70	-0.09	2.50	-0.11
Semi-open grassland	3.10	-0.26	3.60	-0.36	1.00	-0.18	9.00	-0.49
Salt grassland	8.10	0.03	9.20	-0.10	16.20	0.45	1.40	0.01
Riparian vegetation	14.80	-0.49	17.60	-0.40	26.10	-0.50	15.00	-0.48
Road	5.70	0.31	0.90	-0.18	4.40	0.21	3.60	-0.18
Salt marsh	4.80	-0.07	4.20	0.10	0.30	0.01	4.80	0.02
Village	3.50	-0.13	4.20	-0.14	0.30	-0.09	8.10	-0.05
Wetland	9.90	0.17	3.50	-0.11	15.70	0.32	1.70	-0.04

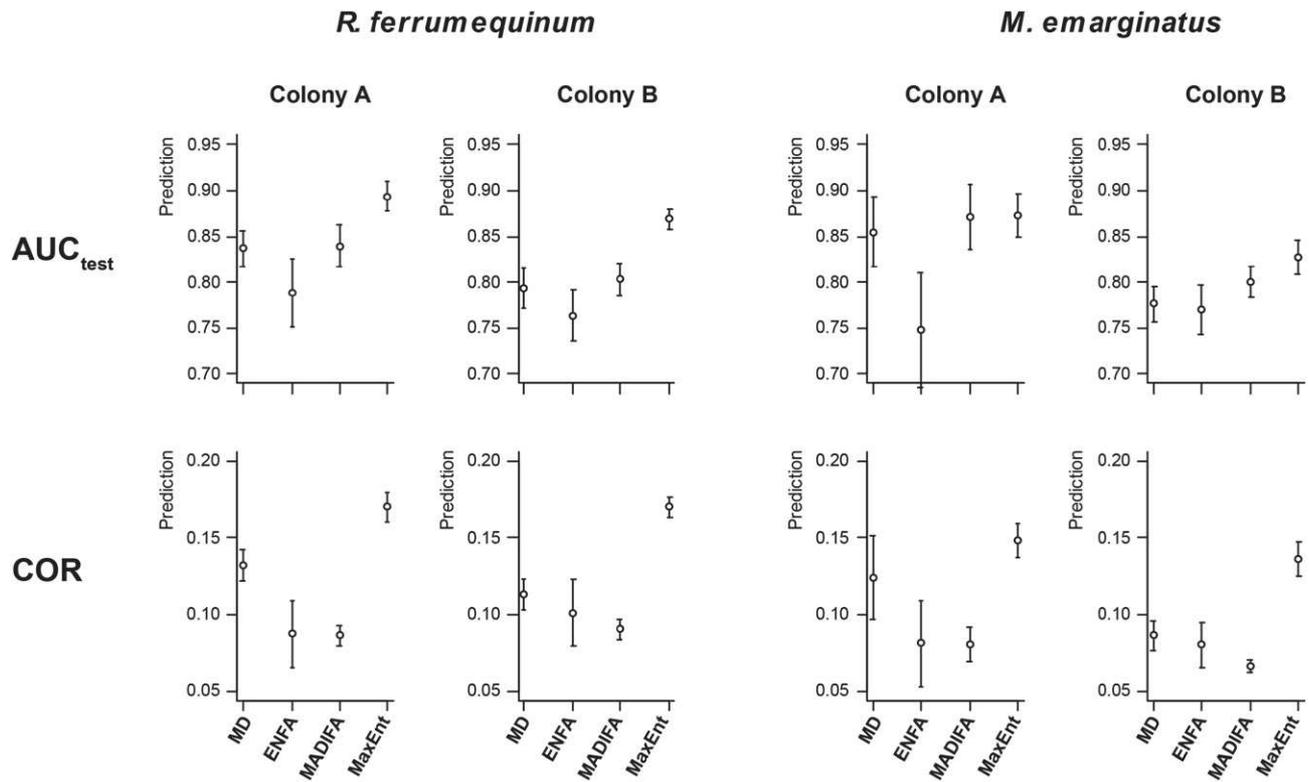


Fig. 2. Comparison of the four presence-only models (Mahalanobis distance (MD), ENFA, MADIFA and MaxEnt) used to create habitat suitability maps for *Rhinolophus ferrumequinum* and *Myotis emarginatus* around the two mixed-species maternity roosts (colonies A and B) for two statistic measures of performance: area under curve (AUC) and Pearson's correlation coefficient (COR). AUC and COR values averages (points) and standard deviations (error bars) were calculated on test data based on 20 replicates ran for each model.

together in the model, except for the prediction of foraging habitat suitability around colony A from the model fitted on colony B for *M. emarginatus*. The predictive performance generally improved when the model used only the most important EGVs in terms of habitat selection (i.e. riparian vegetation, woodland and distance from maternity roost, Fig. 4, Table 4). However, among the four presence-only models tested, only MaxEnt models had an $AUC_{test} > 0.70$ in three of the four cases tested (Table 4). The three other models (MD, ENFA and MADIFA) all had an $AUC_{test} < 0.65$. This result indicates that in our case study MaxEnt models were the best for predicting foraging habitat suitability around another bat maternity roost. In the four cases tested (Table 4), the AUC-values of MaxEnt models are significantly higher compared with the 99% confidence interval of the 99 AUC values obtained with a null-model. This indicates that MaxEnt models differ significantly from what would be expected by chance.

4. Discussion

Our results show that HSMs allow the generation of foraging habitat suitability maps at a fine spatial scale with good predictive performance, and the identification of the EGVs contributing to the foraging habitat selection. To our knowledge, it is the first study to test different HSMs based on presence-only data to compare their predictive power in identifying foraging habitat suitability around bat maternity roosts. Our findings demonstrate variable predictive performance among HSMs. MaxEnt models appear to offer the best predictive performance. These are also the best models at predicting foraging habitat suitability with relatively good performance around another maternity roost using independent radio-tracking locations. Our study also found that at fine spatial scales, the foraging habitat suitability around a maternity roost may depend on a set of a limited number of critical EGVs.

4.1. Bats and foraging habitat selection

Like many other colonial vertebrate species, bats are central-place foragers as they have to return to their maternity roost after a night foraging (Olsson et al., 2008). The suitability of a foraging site is defined by the trade-off between the foraging quality of the site and its distance from the maternity roost, according to the theory of optimal foraging strategy (MacArthur and Pianka, 1966). In line with the study by Rainho and Palmeirim (2011), our results show that the distance from the maternity roost is an important factor in bat foraging habitat selection. During parturition, the energy demands on females are significant; thus females are especially constrained to finding high-quality foraging sites in the immediate vicinity of the maternity roost (Safi et al., 2007; Van Toor et al., 2011). Although microclimate and an absence of human disturbance are important factors in the selection of a house-dwelling maternity roost (Willis and Brigham, 2007) for anthropophilic species such as *R. ferrumequinum* and *M. emarginatus*, the quality of foraging habitat near the maternity roost is also likely to play a decisive role in roost choice.

Consistent with the results obtained in other European studies, *R. ferrumequinum* and *M. emarginatus* were strongly dependent on the availability of deciduous woodland and riparian vegetation within a 5 km-distance of their maternity roost (Flaquer et al., 2008; Flanders and Jones, 2009; Zahn et al., 2010). This dependence on deciduous woodland and riparian vegetation is perhaps even more important in our case study because these habitats are rare in our study area. In fact, the majority of deciduous woodland and riparian vegetation in a radius of less than 3 km of the maternity roost was intensely used as a foraging habitat. Deciduous woodlands are of major importance for insectivorous bats in Europe, probably due to higher prey availability, better wind protection and improved defense against predators when compared to an open habitat. Riparian vegetation is also very attractive

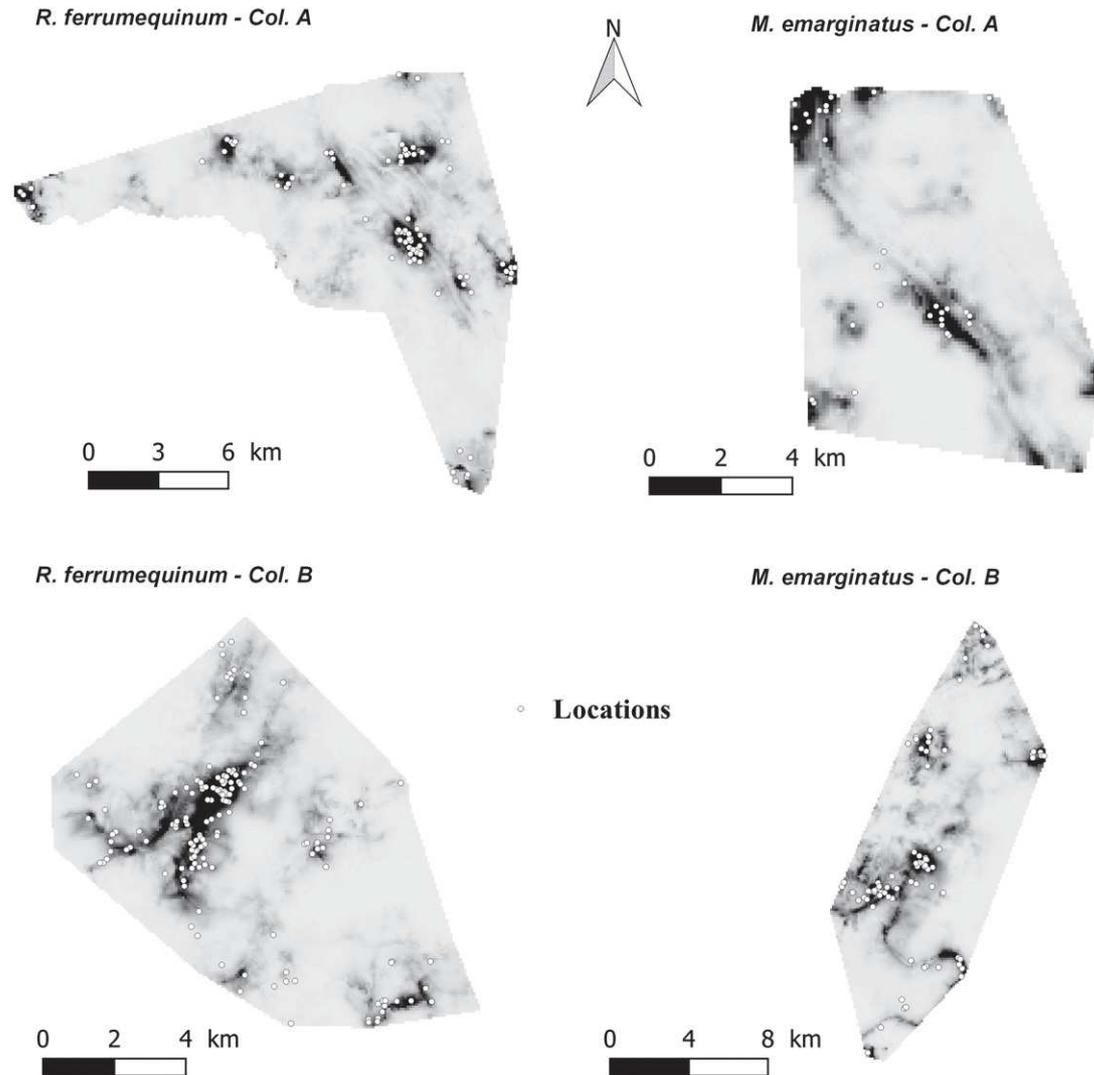


Fig. 3. Foraging habitat suitability maps based on predictions from MaxEnt models for *Rhinolophus ferrumequinum* and *Myotis emarginatus* around the two mixed-species maternity roosts (colonies A and B). Maps were built used 18 eco-geographical variables (EGVs) from 20 run replicates, each time using 70% of presence data (train data) randomly selected, while the remaining 30% (test data) were used to test the predictive performance of MaxEnt models. White circles represent the test data in one of the replicates. Shading indicates levels of model predictions with low habitat suitability in light gray and high habitat suitability in black.

to bats foraging on emergent aquatic insects (Fukui et al., 2006). Furthermore, insect biomass is particularly high in riparian vegetation, with insects emerging from both forest and river ecosystems (Ober and Hayes, 2008). This strong selection pattern of riparian vegetation may be even more apparent in Mediterranean regions, where hot and dry conditions occur during summer, limiting the abundance of prey in other habitat types (Rainho, 2007).

Another critical factor in bat foraging habitat selection around a maternity roost appears to be the vicinity of fresh water. Because of their active flight, bats can lose over 30% of their weight in one night by sudation (Webb et al., 1995). This makes them highly dependent on fresh water for hydration to offset energy and water expenditure, especially in Mediterranean regions. The distance to the closest freshwater body is a major variable influencing foraging habitat selection and must be taken into account in HSMs (Rainho and Palmeirim, 2011).

Our results showed that hedgerows and isolated trees did not appear to influence foraging habitat selection for either species. However, bat species have previously been recorded to be highly dependent on such elements in agricultural landscapes (Brandt et al., 2007; Fischer et al., 2010). In our study area, these two EGVs are quite abundant in the landscape and do not seem to be a limiting factor, which might explain their low importance in foraging habitat selection. Another reason

may be that hedgerows and tree lines in agricultural landscapes are known to protect commuting individuals from predation and wind and to facilitate an individual's orientation around their maternity roost (Verboom and Huitema, 1997). Since our study excluded all presence data representing commuting behavior because the focus was on foraging behavior, it is not surprising that these EGVs did not appear to influence foraging selection. Yet we did note that the commuting locations obtained by radio-tracking suggest that hedgerows and tree lines are indeed used by bats to commute between the maternity roost and different foraging sites (unpublished results).

4.2. Model performance for mobile species at a fine spatial scale

The four HSMs tested in our study (MD, ENFA, MADIFA and MaxEnt) had good predictive performance for mapping bat foraging habitat suitability around a maternity roost (all $AUC_{test} > 0.74$). Nevertheless, we found that MaxEnt outperformed the other three models in terms of its predictive ability, consistent with previous studies (Elith et al., 2006; Hernandez et al., 2006; Rebelo and Jones, 2010). MaxEnt also generally showed less variability in its predictive performance across models compared to the other three models (see standard deviations of Fig. 2). Furthermore, MaxEnt was the best model allowing

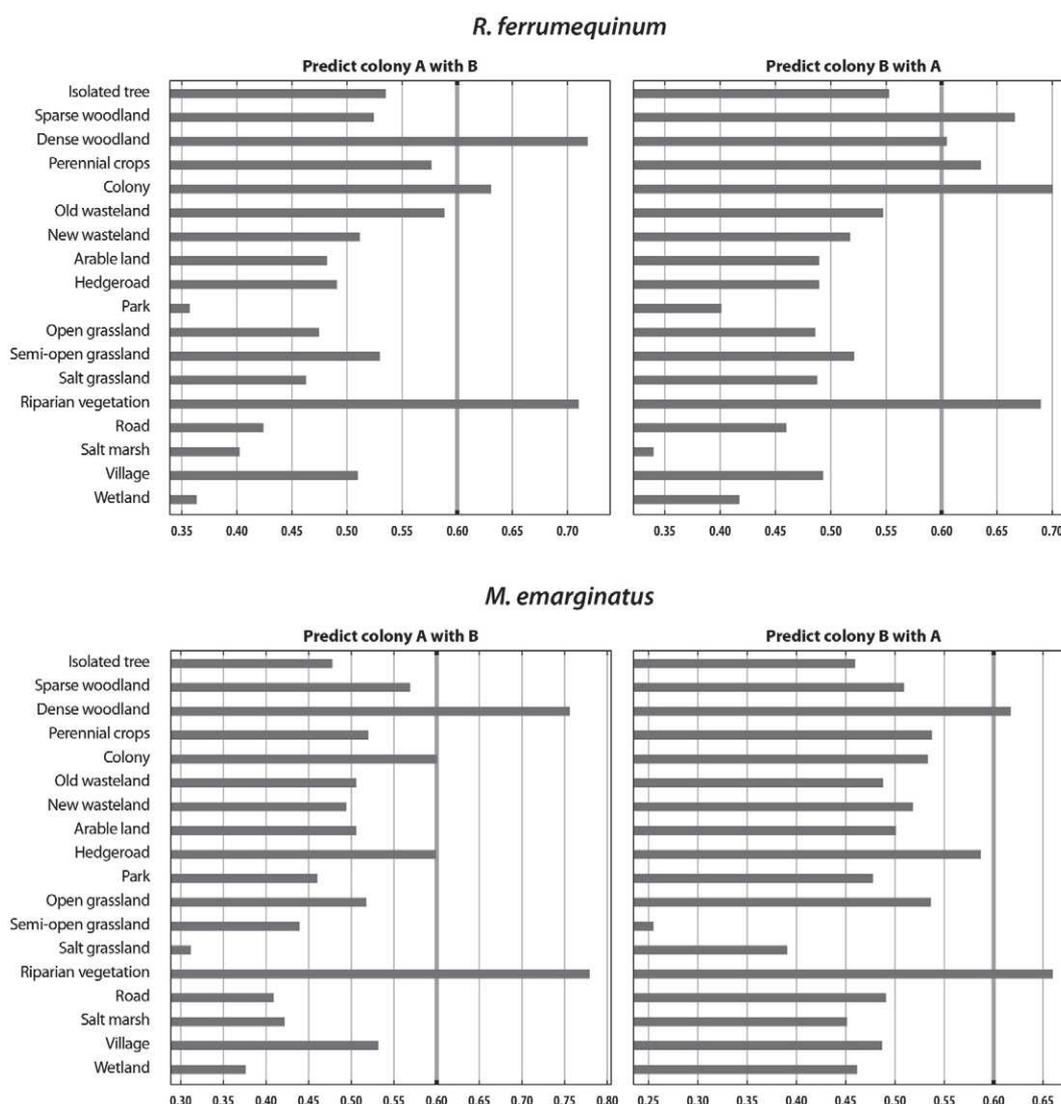


Fig. 4. Representation of the importance of each of the 18 eco-geographical variables (EGVs) used with MaxEnt models for predicting foraging habitat suitability of one colony from the model created for the other colony for *Rhinolophus ferrumequinum* and *Myotis emarginatus*. The x-axis represents the AUC_{test} of the jackknife results for the MaxEnt model using each EGV alone. All locations of one colony were used as train data in the model, and all locations of the other colony as test data. In a second set of MaxEnt models, we have selected all EGVs with an $AUC_{test} > 0.60$ for *Rhinolophus ferrumequinum* and *Myotis emarginatus* (see Table 4).

transferability (Phillips, 2008) for predicting foraging habitat suitability for another independent maternity roost. This apparent low transferability of HSMs can be partly explained by differences in the foraging habitat selection of both species between the two colonies despite the short distance between them (21.5 km). Another reason might be a failure to take into account a significant environmental variable such as the presence of grazed pasture or food prey resources in spatial predictions of foraging habitat suitability. A model's predictive powers are highly dependent on the relevancy of the explanatory variables selected

in the model (Rebello and Jones, 2010). Although grazed pasture is recognized as an important foraging habitat for *R. ferrumequinum* and *M. emarginatus* (Dietz et al., 2013; Flanders and Jones, 2009), we could not include this variable in our HSMs because we did not have a precise map of grazed pasture in the study area. Landscape composition and configuration appear to be the best proxy for describing foraging habitat distribution (Rainho and Palmeirim, 2011). Yet although landscape variables may qualitatively reflect the spatial distribution of prey, they do not give information on either the type of prey insect or seasonal

Table 4

Area under curve (AUC_{test}) and standard deviation (SD) results obtained from the four presence-only models (Mahalanobis distance (MD), ENFA, MADIFA and MaxEnt) used for predicting foraging habitat suitability of one colony from the model created for the other colony for *Rhinolophus ferrumequinum* and *Myotis emarginatus*. In the first step, models used all EGVs with an $AUC_{test} > 0.60$ (see Fig. 4) and finally we have retained the combination of EGVs that maximize the AUC evaluation. The locations of one colony were used as train data in the model, and the locations of the other colony as test data.

Species	Colonies and EGVs selected	MD	ENFA	MADIFA	MaxEnt
<i>R. ferrumequinum</i>	Predict A with B: riparian vegetation + colony	0.62 (0.02)	0.61 (0.02)	0.60 (0.02)	0.72 (0.01)
	Predict B with A: riparian vegetation + colony	0.56 (0.01)	0.50 (0.01)	0.52 (0.01)	0.75 (0.01)
<i>M. emarginatus</i>	Predict A with B: dense woodland + riparian vegetation	0.62 (0.03)	0.63 (0.03)	0.62 (0.03)	0.80 (0.02)
	Predict B with A: dense woodland + riparian vegetation	0.63 (0.02)	0.57 (0.02)	0.64 (0.02)	0.66 (0.02)

rhythms such as insect emergence. Accounting for the spatio-temporal distribution of prey insects across the landscape is a major factor in predicting foraging habitat suitability for insectivorous bats (Fukui et al., 2006; Kusch et al., 2004). Whereas it is surely appropriate to add this type of variable to HSMs, to our knowledge it is difficult to obtain suitable data that explicitly describe spatialized prey resources for insectivorous bat species.

Although HSMs appear to be a promising tool for identifying and mapping foraging habitat suitability within the home range of a maternity roost, they require fine-scale presence data for a species. This data is usually obtained through radio-tracking surveys (e.g. Flaquer et al., 2008; Zahn et al., 2010; Razgour et al., 2011), which are often intrusive for species and require significant financial investment and logistic organization. However, Bellamy et al. (2013) showed that at a local scale, HSMs can also be built with data obtained by acoustic surveys. Based on a limited set of critical EGVs, it may be possible to establish a stratified sampling design for acoustic surveys allowing the prediction of fine-scale distribution of bat foraging habitat suitability. MaxEnt models have the advantage of providing good predictive performance even with a small sample size (Wisz et al., 2008). However, radio-tracking surveys are far more adequate than acoustic surveys in the case of relatively rare species that are difficult to detect with ultrasound detectors (such as all species of the genus *Rhinolophus*) or that pose difficulties of acoustic identification (as in genus *Myotis*). For future studies, it would be interesting to compare the predictions between HSMs using these two types of surveys.

4.3. Conservation implications

The characterization and mapping of foraging habitat suitability around maternity roosts are two major concerns for planning conservation actions to protect threatened bats (Fenton, 1997; Russo and Jones, 2003). Our results showed that HSMs can successfully predict foraging habitat suitability at a fine spatial scale and can thus be useful tools for environmental managers in defining appropriate conservation guidelines for foraging habitats. However, different HSMs still need to be tested on other bat species and in other landscape contexts to assess their robustness to correctly predict foraging habitat suitability around maternity roosts. Our study demonstrated the critical role of deciduous woodlands and riparian vegetation around maternity roosts in foraging habitat selection for *R. ferrumequinum* and *M. emarginatus*. Therefore, habitat management around maternity roosts should aim to improve or restore deciduous and riparian forests, which may equally be beneficial for the whole bat community (Russo and Jones, 2003).

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