Biological Conservation 317 (2026) 111797

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

# Assessing the benefits of part-night lighting on a tropical bat species endemic to Reunion Island☆

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ARTICLE INFO

*Keywords:*
Activity rhythm
Bats
Conservation
Light pollution
Part-night lighting
Passive acoustic monitoring

ABSTRACT

Artificial light at night (ALAN) is recognised as an emerging threat to global biodiversity but no technical mitigation strategy can prevent all impacts on ecosystems. Consequently, the most effective measure remains turning-off lights whenever and wherever possible. However, few studies, all carried out in temperate environments, assessed the effectiveness of Part-Night Lighting (PNL) and the benefits that might result from changes in switch-off times. On the tropical Reunion Island, where ALAN is increasing exponentially, we assessed the sensitivity of an endemic bat species (*Mormopterus francoismoutoui*) to light, and the effectiveness of PNL in reducing the potential impacts on this species, depending on the switch-off times implemented. We took advantage of the modification of an existing PNL during a month-long event, consisting in switching off lights two hours earlier than the rest of the year. By carrying out an acoustic monitoring of bat echolocation calls, using a Before-After Control-Impact Paired protocol, we showed that bats were attracted to lit sites, especially at the beginning and end of the night, when the lights were on. When the lights were switched off earlier in the evening, there was no longer any impact on bat activity and rhythm, although a tendency toward greater activity at the end of the night in lit sites persisted in clear weather. This provides important insights, encouraging extensive use of PNL, ideally with even earlier switch-off times, as a promising measure for mitigating ALAN effects on this endemic species whose overall population vulnerability is still unknown.

## 1. Introduction

Artificial lights at night (ALAN) is a global threat to biodiversity (Hölker et al., 2010; Jägerbrand and Spoelstra, 2023). ALAN impacts organisms at multiple biological levels, from molecules to populations, with effects extending even to ecosystem functioning. Many mechanisms are at play, such as attraction and repulsion of individuals, physiological and biological rhythms disturbances, changes in species interactions, decreasing fitness, *etc.* (*e.g.*, Cravens and Boyles, 2019; Degen et al., 2016; Jägerbrand and Spoelstra, 2023; Van Doren et al., 2017).

This emerging threat has been extensively studied by biological

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☆ This article is part of a Special issue entitled: ‘Dark night conservation’ published in Biological Conservation.

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https://doi.org/10.1016/j.biocon.2026.111797
Received 24 July 2025; Received in revised form 29 January 2026; Accepted 10 March 2026

sciences, leading to the identification of key lighting parameters that can be modified to reduce ALAN impacts, including adjusting light intensity, orientation, distribution, spectral composition and duration (Gaston et al., 2012; Jägerbrand and Spoelstra, 2023; Stone et al., 2012). However, no single strategy can fully eliminate the impacts on biodiversity, as different species often exhibit varied sensitivities to light parameters. For example, moths are more attracted to blue and ultraviolet wavelengths, whereas beetles are more attracted to red wavelengths (Owens and Lewis, 2018). The selection of appropriate lighting parameters and thresholds is therefore complex and depends on the specific taxa being targeted.

Bats, as nocturnal species directly exposed to ALAN, have been the focus of many studies on its impacts on biodiversity. A wide range of effects of light pollution on bats has been documented for insectivorous species (Voigt et al., 2021) and, to a lesser extent, for frugivorous (*e.g.*, Hoyos-Díaz et al., 2018; Lewanzik and Voigt, 2014; Murugavel et al., 2023) and nectarivore species (*e.g.*, Dzul-Cauich and Munguía-Rosas, 2022). For insectivorous species, this includes impacts at their roosts (*e.g.*, delayed emergence, reduced reproduction success, abandonment of roosts; Boldogh et al., 2007; Rydell et al., 2021), in their flight corridors (*e.g.,* change in flight patterns in favour of cluttered environments, impassable gaps, delayed onset of commuting behaviour; Barré et al., 2021; Hale et al., 2015; Stone et al., 2009), and at their drinking and foraging sites (*e.g.*, repulsion for some species – probably due to a perception of higher predation risks, attraction to light sources for others – due to the aggregation of insects around them, disturbances of activity rhythms; Azam et al., 2018; Hermans et al., 2024; Mariton et al., 2022; Rydell, 1992). In this context, it seems urgent to mitigate the effects of light pollution on bats.

For the same light intensity, red light has been proposed to mitigate the impact of light on bat abundance compared to green and white lights (Spoelstra et al., 2017). However, recent studies carried out at the same sites have shown that red wavelengths have as negative an effect as blue and green wavelengths on the flight behaviour of individuals, and their ability to cross illuminated areas (Barré et al., 2023, 2021). Without distinguishing between wavelengths, other studies have shown that even extremely low intensities (*i.e.*, below one lux) can still have an impact on bats, raising concerns about the effectiveness of measures focused solely on reducing light intensities (Azam et al., 2018; Mariton et al., 2022). Additionally, variations in light intensity can have different impacts on bats depending on the wavelength (Kerbiriou et al., 2020). Consequently, the best technical option remains to turn off lights as much as possible, either by removing unnecessary light sources, or by limiting the duration of lighting.

Part-night lighting (PNL) is increasingly adopted in France as part of local public policies aimed at balancing energy saving, dark sky representation and biodiversity conservation. Many municipalities now switch off public lighting when human activity is low. In mainland France, approximately 40% of municipalities have implemented PNL (ADEME, 2021). Despite its growing popularity, few studies have assessed the benefits of this measure on biodiversity, likely due to the absence of baseline data prior to its introduction, and the challenges of conducting experiments across different administrative units.

In Europe, three studies suggested that current PNL schemes do not adequately cover the range of bat activity, especially because light switch-off occurs too late in the evening (Azam et al., 2015; Day et al., 2015; Hooker et al., 2022). Indeed, human needs for light are generally high when most European bat species reach their peaks of activity: the first during the first two hours after sunset, following insect emergence, and the second, smaller peak at the end of the night (Mariton et al., 2023). However, the effect of earlier switch-off times — than what is already done in existing PNL schemes — has not yet been evaluated, even though it seems to be a promising way of reducing ALAN impacts on biodiversity. This is particularly important in regions where bat responses to ALAN have been little studied, such as in tropical areas. Some of these regions are experiencing a considerable increase in population and, in turn, in artificial lighting, as on Réunion Island — a French overseas territory located in the south-west of the Indian Ocean — where the population has grown from 250,000 in the 1950s to over 885,000 in 2024. Between 1996 and 2020, based on radiance measurement by DMSP and VIIRS satellite instruments, Chevillon et al. (2022) showed that it increased by 60% in the island.

On Réunion Island, PNL is less systematically applied year-round than in mainland France, where many municipalities opt for PNL throughout the year mainly for economic and sometimes ecological reasons. Located in the south of Réunion Island, Saint-Joseph is one of the few municipalities that implements a year-round PNL scheme. In contrast, most of the other municipalities implement a time-limited, ecologically targeted PNL initiative each austral autumn, as part of the *Nuits sans lumière* (“*Nights without light*”) campaign. It was launched in 2009 by the Réunion Society for Ornithological Studies (SEOR) in partnership with the Réunion National Park and local authorities to protect fledging petrels from fatal light-induced disorientation during nearly a month starting on early April (Chevillon et al., 2022). To date, 19 of the island's 24 municipalities are taking part in this event. While its focus remains seabird conservation, the campaign also provides a valuable opportunity to assess the broader ecological impacts of PNL — including changes in its switch-off times — on other species, such as the island's endemic bats.

The Réunion free-tailed bat (*Mormopterus francoismoutoui* Goodman et al., 2008) is one of the only three known bat species on the island and its only known endemic terrestrial mammal species. This species is widely distributed over the island and roosts both in natural (*e.g.*, rock crevices, caves) and anthropogenic settings (*e.g.*, bridges, roofs) (Goodman et al., 2008). According to a study conducted by Aguillon et al. (2023) on roosts (maternity roosts and other roosts), colonies are ranging from a few dozen to several thousand individuals (even reaching 100,000 individuals). Pregnancy, parturition and lactation occur late June to late September while males are mainly reproductively active from mid-January to the end of April (Aguillon et al., 2023). Based on their acoustic ecology, this insectivorous species could be adapted to a wide variety of habitats — from open to edge and even closed environments — both in natural and urbanised settings (Barataud and Giosa, 2013). We hypothesised that *M. francoismoutoui* would increase its activity near ALAN to exploit ecologically trapped insects that are attracted to light, as observed in opportunistic European species sharing similar traits and foraging strategies, such as the *Pipistrellus* genus (Voigt et al., 2021). Although Barataud and Giosa (2013) suggested a potential link between high activity of *M. francoismoutoui* and proximity to lit urban areas, the species' response to ALAN has yet to be investigated.

We took advantage of the earlier switch-off times introduced in the permanent PNL scheme of Saint-Joseph during the *Nuits sans lumière* to assess their effects on *M. francoismoutoui*. We measured *M. francoismoutoui* activity through an extensive acoustic monitoring of its echolocation calls, using a Before-After Control-Impact Paired (BACIP) protocol. Before the adjustments, we compared the abundance and activity rhythm of this species between unlit control sites and paired treatment sites where permanent PNL was implemented. After the implementation of the adjustments, we repeated the same comparisons, with earlier light switch-off times on the sites with PNL. We expected that the earlier light switch-off times would reduce light pollution impacts on this species' activity.

## 2. Material and methods

### 2.1. Study area

Réunion Island is a 2512 km$^2$ tropical volcanic island in the western Indian Ocean (21°S, 55°E). We focused on Saint-Joseph a municipality with a homogeneous landscape of forests (27%), shrub and herbaceous vegetation habitats (25%), agricultural areas (25%), impervious and urban areas (8%) and water bodies (3%). According to the VIIRS-DNB databases, radiance has increased by approximately 63% in this municipality over the last few years (2015–2024, see Fig. S1). The densely urbanised coastal area, with higher levels of ALAN and no PNL schemes at the time of the experiment, was excluded to focus on the upper part of the municipality (from 100 to 1300 m above sea level). This area offers a more natural landscape favourable to bats, more diffuse ALAN and a homogeneous lighting strategy (Fig. 1A).

### *2.2. Sampling design*

We recorded bat activity at 30 pairs of sites consisting of a site with PNL (treatment) and an unlit site (control). One "pair" included only a treatment site due to inconsistencies between expected and actual lighting (theoretically control unlit site that turned out to be lit) (Fig. 1A, Table S1). The treatment and control sites within each pair were selected so that the landscape composition was as similar as possible in terms of

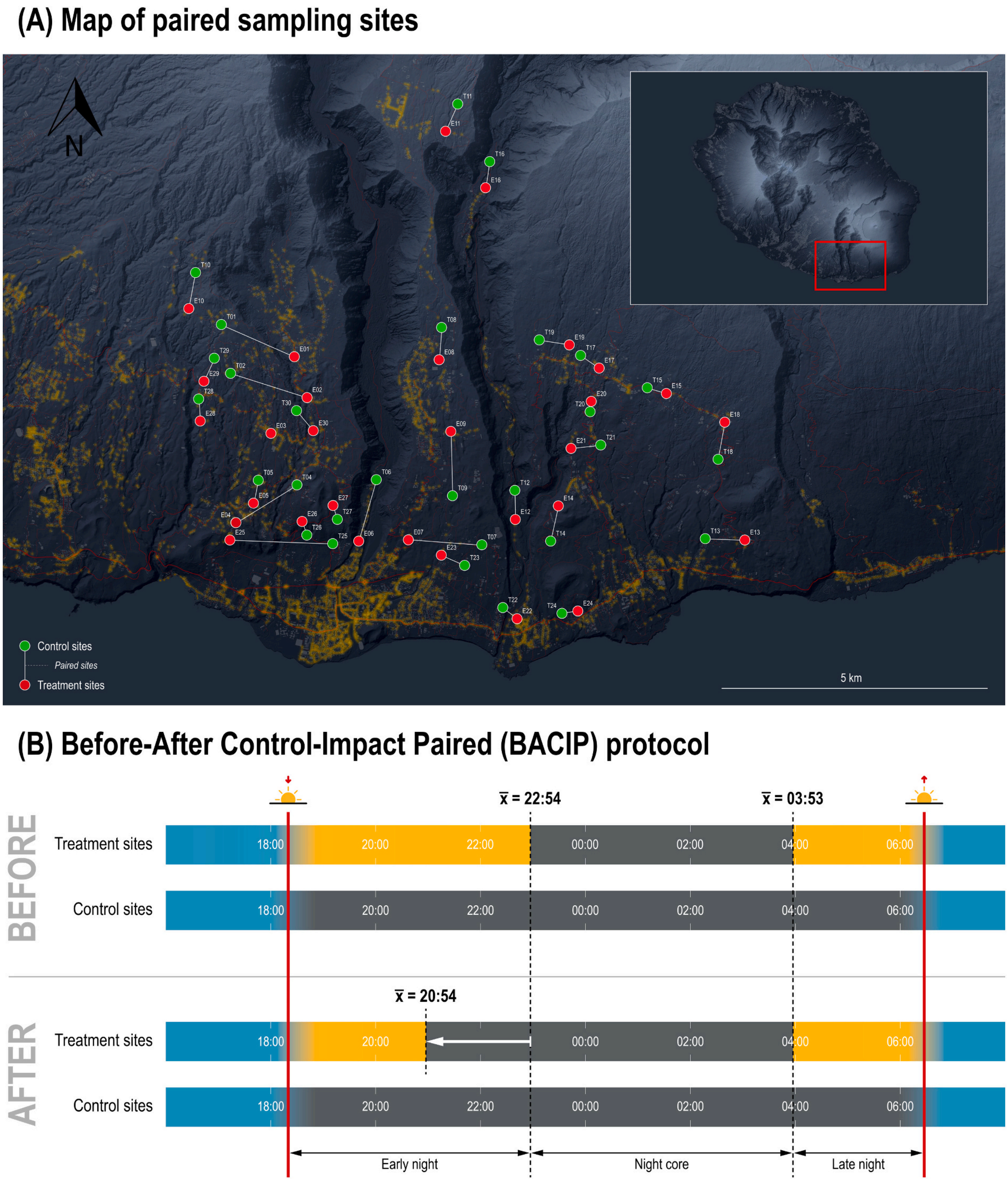


**Fig. 1.** (A) Map of acoustic monitoring sites, composed of paired lit (treatment, in red) and unlit (controls, in green) sites (ALAN is shown in a stylised manner based on the coordinates of public lighting points, the colour used does not represent the actual colour temperatures of the light sources) and (B) schematical view of the protocol consisting of a comparison between lit and unlit sites, before and after the modification of the PNL schemes. Dotted lines represent the temporal variations in the onset and the end of light extinction across sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proportions of crops, grasslands, impervious areas and forests around the sites (see Fig. S2 for details). Paired Wilcoxon tests showed only one significant difference: higher proportions of impervious areas at treatment sites compared to control sites. Nevertheless, the distribution of the proportion of impervious areas remains highly overlapping between treatment and control sites, and is mainly limited to values between 10 and 28%. We therefore assumed that the standardisation of the landscape was acceptable. Furthermore, the BACIP model protects against such landscape variation by comparing differences in bat responses between treatment and control sites before and after the extension of PNL, while incorporating a random effect on the pair in the models (see section 2.4), so that the landscape remains constant throughout the comparisons.

Both sites within each pair were sampled simultaneously before and after the modification of the PNL scheme at the treatment site (hereafter "before" and "after" periods, respectively). Sampling took place over 13 consecutive nights, from 3 to 16 April 2022, with 5 or 6 pairs sampled each night (Table S2). The aim was to test the effect of these modifications at the treatment sites compared to the control sites, which remained unchanged, using a BACIP protocol (Fig. 1B).

The PNL scheme in the before period consisted of the lighting:

- being switched off between 10:30 to 11:12 pm depending on the site (mean = 10:54 pm; SD = 10 min),
- being switched on between 03:30 to 04:19 am (mean = 3:53 am; SD = 19 min).

The adapted PNL scheme in the after period consisted of the lighting:

- being switched off from 08:30 to 09:15 pm (mean = 08:54 pm; SD = 14 min, mean difference between the before and after periods = −2 h00; SD = 20 min),
- being switched on at the same time as for the before period for nine sites, and being slightly modified for the others sites (either switched back on earlier or later) and ranging from 2:55 to 04:15 am depending on the site (mean = 3:35 am; SD = 31 min, mean difference between the before and after periods = −21 min; SD = 41 min) (Fig. 1B).

All streetlights were activated at sunset. We sampled two types of streetlights, lighting-emitting diodes (LED) and high-pressure sodium (HPS) lamps, at 19 and 11 treatment sites respectively (Table S1). Light height was consistent across sites (between 6 and 10 m for all treatment sites, except one at 18 m, mean = 8.9 m, SD = 1.57 m).

### 2.3. *Bat acoustic sampling*

We recorded bat echolocation calls with AudioMoth loggers (firmware version 1.6.0) from 30 min before sunset to 30 min after sunrise. One logger per site and date was used, placed vertically 1.5 m above the ground, between 0 and 19 m (mean = 3.2 m; SD = 5.3 m) or between 41 and 641 m (mean = 273.5 m, SD = 156.6 m) from the nearest streetlight at the treatment and control sites, respectively. All sounds were recorded continuously between 8 and 48 kHz (sample rate = 96 kHz), with a low-medium gain, a 1% amplitude threshold, and a 2 s minimum trigger duration.

Since it is currently impossible to distinguish individual bats from their echolocation calls, we measure activity based on the number of bat passes. As is commonly done in bat acoustic studies, we defined a bat pass as one or several echolocation call(s) within a 5-s interval (Millon et al., 2015).

Since no automatic classifier exists for our model species and its echolocation calls are very similar to those of several European species (*Hypsugo savii*, *Miniopterus schreibersii* and *Pipistrellus spp.*) (Barataud and Giosa, 2013), we used the European classifier Tadarida (Bas et al., 2017) to assign identifications to the recordings. All recordings classified as one of these species were considered as *M. francoismoutoui.* To validate this approach, we randomly checked 233 detections classified as *M. francoismoutoui* across Réunion Island, balancing the verification process across the software's confidence score classes, sites and days. Finally, we applied a filter based on Barré et al. (2019) to retain only detections with a confidence score from the automated identification software of at least 0.5, eliminating the majority of false positives (by doing so, only detections with a probability of being correct greater than 0.9 are considered, see Fig. S3 and Table S3 for more details).

### 2.4. *Statistical analysis*

#### 2.4.1. *Effects of PNL schemes on bat activity levels*

To test whether bat activity was influenced by PNL schemes, we compared activity between treatment and control sites over different parts of the night, for the before and after periods. We defined night parts based on the switched-off and on times of the treatment sites:

- the "early night" part: from sunset (6:15 pm) to the mean time of extinction during the before period (10:53 pm) (fully lit and partially lit during the before and after periods, respectively),
- the "late night" period: from the mean time at which the lights were switched back during the before period (03:34 am) to sunrise (6:30 am) (lit during both periods),
- the "night core": between the "early" and "late night" parts,
- the whole night (Fig. 1B).

To ensure the robustness of the results, we reproduced these analyses using a more conservative division of the night based on the before period: the "early night" part from sunset to the earliest switch-off time (10:30 pm), the "core night" part from the latest switch-off time (11:12 pm) to the earliest switch-on time (03:00 am), and the "late night" part from the latest switch-on time (04:19 am) to sunrise.

For each night part and for both periods, we modelled the number of bat passes using Generalized Linear Mixed Models (GLMM, R package *glmmTMB*) associated with a negative binomial family (quadratic parameterization). We modelled it in relation to three light pollution metrics in different models: the type of site (treatment and control), the distance to the nearest streetlight, or to the lamp type (LED and HPS) (Eq. 1). We did not include moon phase in our models because our monitoring session covered less than one complete lunar cycle and high percentage of heavy cloud cover were recorded, especially at the beginning and end of the monitoring (as shown by Mariton et al. (2022), cloud cover can mask moonlight and reduce its potential effects on bat activity) (Fig. S4). Since precipitation strongly varied over the nights and between the before and after periods, with non-negligible hourly cumulated values (Fig. S5), we included the cumulated hourly precipitation recorded over the part of the night considered (obtained from a Météo France station located in the middle of the study area), in interaction with the light explanatory variable. For the sake of clarity and parsimony, if the model without the interaction had a lower Second-order Akaike Information Criteria (AICc), the interaction was removed. Numerical explanatory variables were scaled.

We used the pair identifier as a random effect to account for the structure of the sampling design. Although several pairs were sampled each night, we did not include date as a random effect since the best random effect structure on the basis of the AICc was the pair identifier alone. We checked model residuals using the R package *DHARMa* (Hartig, 2024).

$$\text{Number of passes}_{\text{Part of the night}} \sim \text{Light pollution metric}^{*}\ \text{Cumulative Precipitations}_{\text{Part of the night}} + (1|\ \text{Pair}) \tag{1}$$

*With:*

- *Part of night = "early night", "night core", "late night" or "whole night"*
- *Light pollution metric = "type of site" ("Treatment" or "Control"), "distance to the nearest streetlight" or "lamp type" (LED or HPS)*
- *The interaction term was kept only if the AICc was lower when included.*

### 2.4.2. *Effects of the PNL schemes on bat activity rhythms*

To visualise bat activity rhythms throughout the night depending on PNL schemes, we modelled the number of bat passes in ten-minute intervals according to the type of site (treatment *vs* control), the smoothed number of minutes after sunset, and their interaction, using Generalized Additive Mixed Models (GAMM, R package *mgcv*) with a negative binomial family. To account for the sampling design structure, we included the pair identifier and the date as random effects. We applied this model on the before and after periods separately.

To test whether PNL schemes influenced bat activity rhythms, we ran the same models as in section 2.4.1, replacing the response variable by the median time of bat passes in the first and second half of the night. This metric is a robust descriptor of activity distribution, particularly its peaks, and is not sensitive to extreme events (unlike the first or last calls of the night) (Mariton et al., 2023).

## 3. Results

### 3.1. *Bat survey*

We recorded 303,894 passes of *M. francoismoutoui* over the sampling period, with an average of 2202 passes (SD = 2405) per survey (*i.e.*, per combination of sites and dates surveyed, *N* = 138). At the unlit control

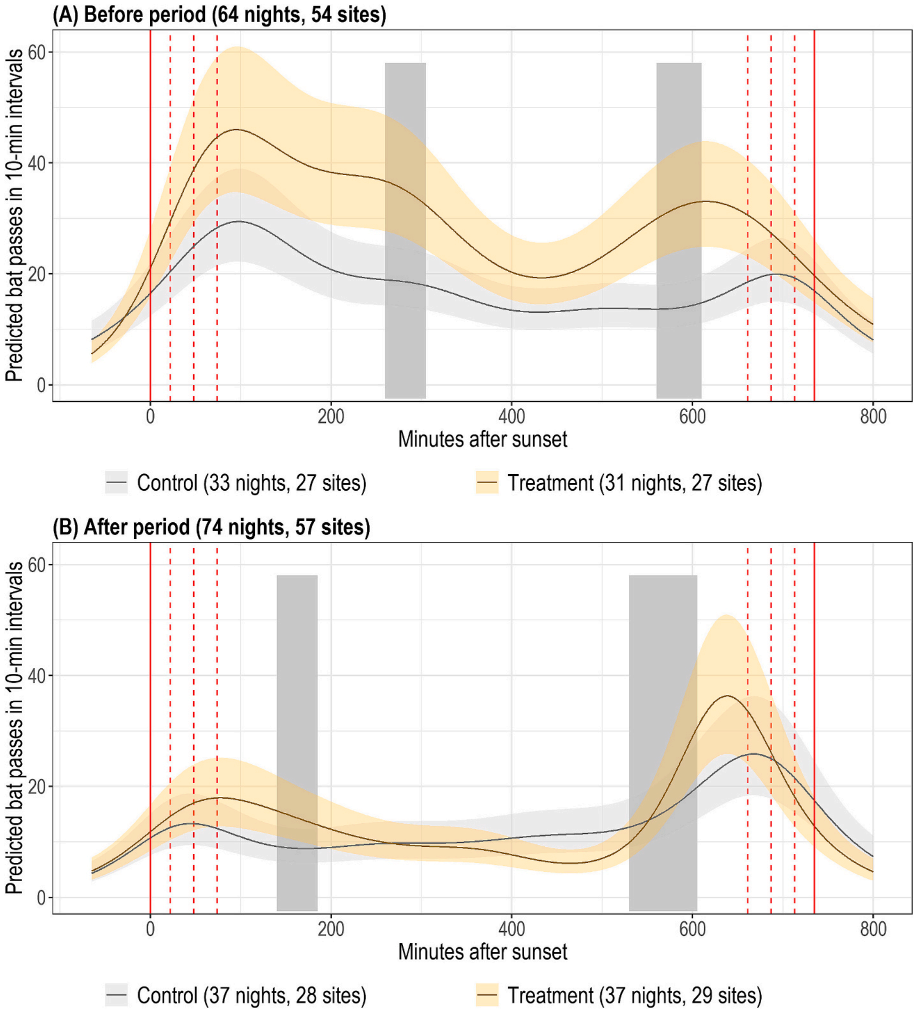


**Fig. 2.** Predicted number of bat passes from GAMM in ten-minute intervals in relation to the time elapsed since sunset for control (grey) and treatment (yellow) sites before (A) and after (B) the modification of the PNL schemes. 95% confidence intervals are used. Red solid lines show sunset and sunrise times. Dotted lines show civil, nautical and astronomical sunset, and astronomical, nautical and civil sunrise. Vertical grey areas represent the time variation of the switch-off and on times depending on sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sites, on average 2049 passes (SD = 1769, *N* = 33) and 1541 passes (SD = 1559, *N* = 37) were recorded per survey in the before and after periods, respectively, while 3448 passes (SD = 3360, *N* = 31) and 1955 passes (SD = 2349, N = 37) were recorded per survey at the lit treatment sites in the before and after periods, respectively. *M. francoismoutoui* was recorded in every survey.

### 3.2. *Bat activity rhythm*

Bat activity followed a bimodal pattern, with peaks in the early and late night regardless of the site type (treatment or control) (Fig. 2). In the before period, the first peak in activity (just after sunset) was greater than the second one (just before sunrise), whereas, during the after period, it was the opposite.

### 3.3. *Effects of the PNL schemes on the activity of bats*

During the before period, bat activity was significantly higher in treatment sites in the early part of night (estimated coefficient $\beta = 0.48$, *p*-value = 0.03, predictions were 62% higher), late part of night ($\beta = 0.55$, p-value = 0.03, 73% higher) and during the whole night ($\beta = 0.46$, p-value = 0.03, 59% higher) (Figs. 2A & 3A). We did not detect any change in activity levels in relation to the distance to the nearest streetlight or lamp type (Fig. S6).

Regarding the median time of activity at the start and end of the night, light pollution metrics alone had no significant effect (Fig. S7). However, we detected a significant effect of the interaction between precipitation and the type of site during the first half of the night (p-value = 0.003). At treatment sites, the heavier the rainfall, the earlier the median time of activity, whereas the activity rhythm of bats was practically unaffected by rainfall at control sites (Fig. 4A & B).

During the after period, we no longer detected significant differences in the early part of night and throughout the night between treatment and control sites (Figs. 2B & 3B). The level of activity at the end of the night was significantly influenced by the interaction between precipitation and the type of site (p-value = 0.02). The heavier the rainfall, the weaker the trend toward a positive effect of the treatment site on activity, with activity tending to be higher at control sites during heavy rain (Fig. 5A & B). Activity during the core of the night was also significantly influenced by the interaction between precipitation and site type (p-value = 0.01). The heavier the rainfall, the weaker the trend toward a positive effect of the control sites on activity (Fig. 5C & D). Distance to the nearest streetlight and lamp type alone did not have any major effect on bat activity level. During the core of the night, the interaction between precipitation and distance from the nearest streetlight was significant (p-value = 0.04), with greater activity at sites far from streetlight during low rainfall (Fig. 5E & F).

Regarding the median time of activity at the beginning and end of the night, no significant change was detected between treatment and control sites during the after period, according to the distance from the nearest streetlight or lamp type (Fig. S7).

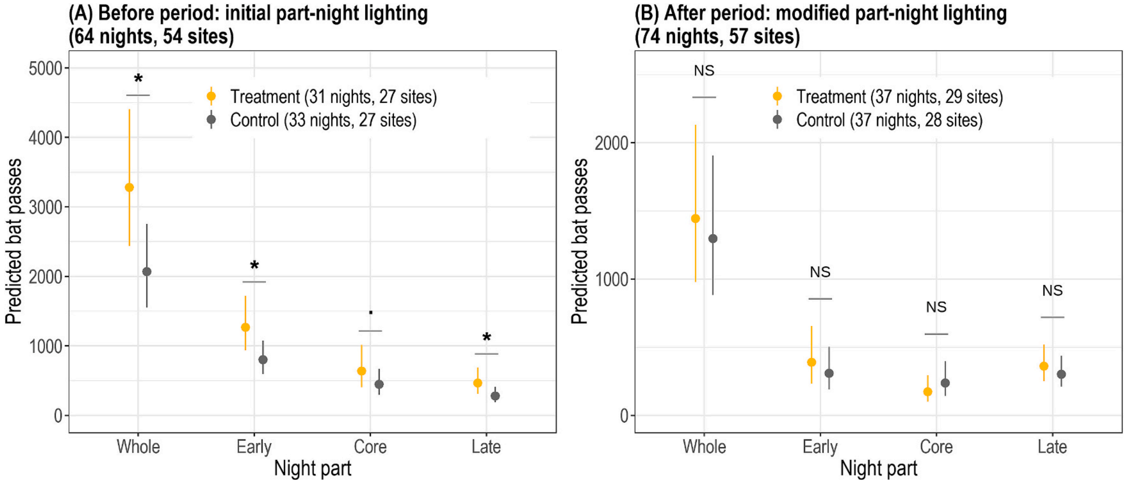
Overall, precipitation had a significant negative effect on bat activity during both periods, affecting activity significantly in 11 out of 24 models.

Model coefficients supporting these results are in Tables S4 & S5. Finally, the results obtained using a more conservative night division are very similar (Table S6).

## 4. Discussion

The study reports, for the first time, the sensitivity of *M. francoismoutoui*, a tropical bat species endemic to Réunion Island, to ALAN, and the possible effectiveness of part-night lighting (PNL) as a mitigation strategy. Overall, as we predicted, *M. francoismoutoui* was attracted to lights when and where they were switched on. The activity rhythm of this species was bimodal in both lit and unlit conditions. It included an activity peak at the beginning of the night, before the lights were switched off as part of the regular PNL implemented in Saint-Joseph, and another before sunrise after the lights were switched back on. In this context, bat activity was higher throughout the night, at the beginning and end of the night at lit treatment sites than at unlit control sites. When the switch-off times were brought forward two hours earlier as part of the adapted PNL, the impact of ALAN on activity levels was no longer perceptible throughout the night and at the start of the night, with activity at lit treatment sites becoming similar to that at the unlit control sites. At the end of the night, the attractive effect of light compared to unlit control conditions was however still observed, unless precipitation was heavy, which is not surprising since, unlike the switch-off time, the switch-on times were not substantially modified.

This study provides important insights in the context of an exponential increase of light pollution on Réunion Island. It shows that, to effectively mitigate ALAN impacts on this endemic species, PNL scheme must provide an extended period of darkness that covers at least part of this species' activity peaks at the beginning and end of the night. This entails switching off lights earlier in the evening and switching them back on later in the morning. These results are all the more important as the vulnerability of this species' population is still unknown.



(A) Before period: initial part-night lighting
(64 nights, 54 sites)

(B) After period: modified part-night lighting
(74 nights, 57 sites)

**Fig. 3.** Predicted number of bat passes from GLMM according to the night parts for treatment and control sites (A and B, respectively). Annotations show significance levels obtained using type-II tests (* $P < 0.05$;. $0.05 < P < 0.1$; NS non-significant), 95% confidence intervals are used.

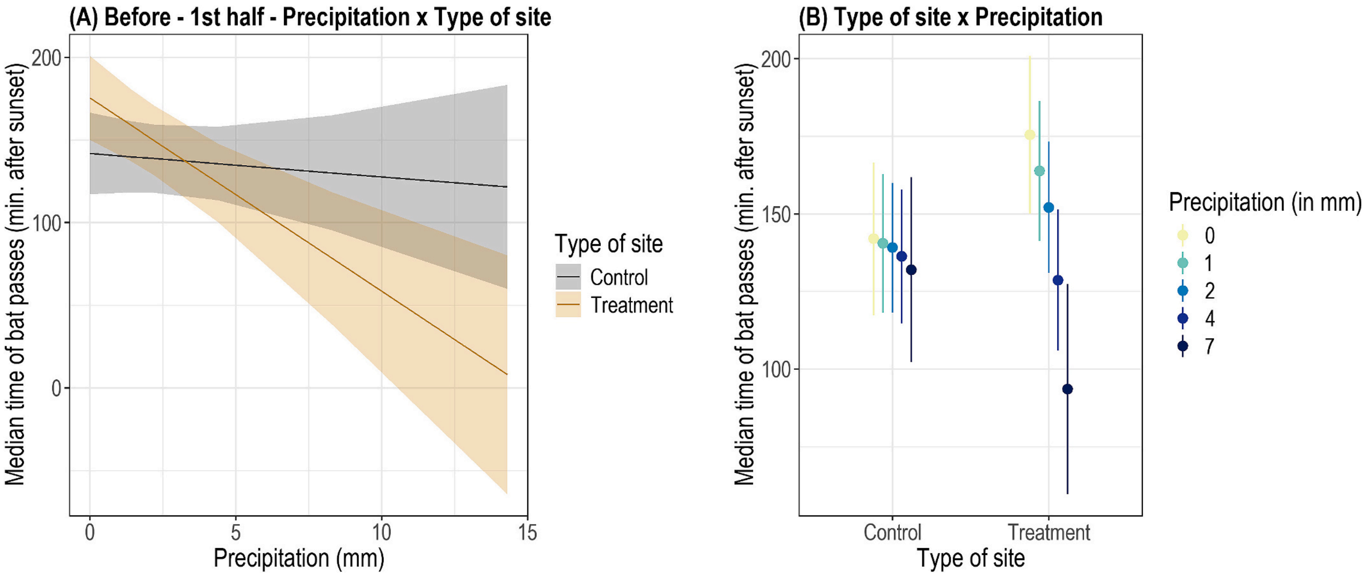


**Fig. 4.** Predicted median time during the first half of the night according to the precipitation and the type of site.

### 4.1. *Light attractive effects*

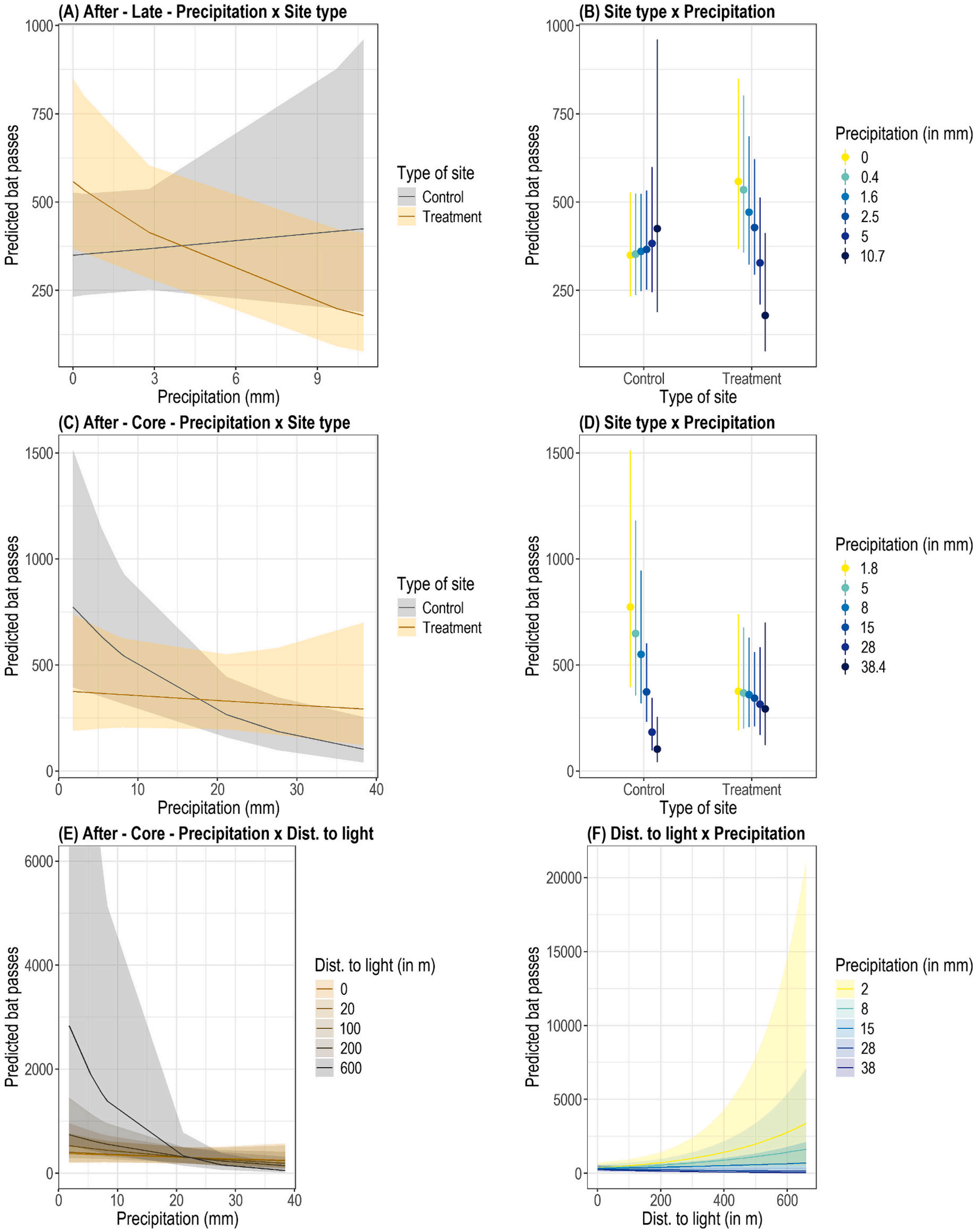
This study highlights the attractive effect of light on *M. francoismoutoui*. Activity levels were higher at lit sites when the lights were on (*i.e.*, throughout the night, at the beginning and end of the night before the modification of the PNL schemes and again at the end of the night after the modification, provided rainfall was not so great as to prevent bat activity) than at unlit sites. However, except for an interaction between precipitation and the distance to the lamps during the core of the night after the modification of the PNL schemes, no effect of distance to lamps or lamp type variables was detected on activity. It may be explained by a distance gradient studied too coarse (0 to more than 600 m), only considered in a linear manner, which could prevent the detection of variations in abundance, that, according to the literature, can occur over relatively short distances of less than 50 m (Azam et al., 2018). Similarly, we did not know the light intensity of the lamps studied, yet this is a parameter that can strongly bias the comparison of the effect of lamp types on bat activity (Kerbiriou et al., 2020).

The attraction of *M. francoismoutoui* to light sources is consistent with the opportunistic nature of this species – which can forage in a wide diversity of habitats – suggested based on its acoustic ecology (Barataud and Giosa, 2013) and diet plasticity (Dietrich et al., 2025). Indeed, while it has been shown that certain bat species, especially narrow-space foraging species, always avoid light sources – probably because their flight strategy makes them more vulnerable to predation risks, which may be perceived as higher in the vicinity of light –, opportunistic edge- and open-space-foraging species, are known to be attracted to ALAN when hunting (Rydell, 1992; Voigt et al., 2021). This positive phototaxis can be explained by aggregations of insects near light sources, providing predictable food resources for opportunistic bat species whose flight strategy makes them less susceptible to predation (Voigt et al., 2021). In lit conditions, these light-tolerant species could also integrate visual information in addition to echolocation, enabling them to approach their prey more efficiently (Stidsholt et al., 2025). The accuracy of our prediction of this species' response to ALAN, made by analogy with European species sharing similar foraging and acoustic adaptations (light-tolerant *Pipistrellus* species), validates that bat traits can be good predictors of bat response to anthropogenic pressures for species that are poorly known (Froidevaux et al., 2023), even if the ecological contexts are very different (climate, food webs, *etc.*).

However, such attractive effects should not hastily be considered as positive, as they can be a component of strong disturbances in the functioning of populations and ecosystems. Even though light-tolerant bat species are locally attracted to light sources, at landscape scale their activity is lower in illuminated landscapes (Azam et al., 2016; Mariton et al., 2022). Indeed, concentration of bats above a certain level can reduce foraging success, even though prey is more accessible and more abundant close to light sources (Krivoruchko et al., 2024). Light pollution can also be responsible for a reduction of food resources as insect populations can decline dramatically when exposed to ALAN (Owens et al., 2019). By attracting insects massively, light sources can also cause them to desert surrounding dark areas, creating a “vacuum cleaner” effect (Boyes et al., 2020). Reshaped competitive interactions between insectivorous species near light sources might prevent some species from accessing prey (Salinas-Ramos et al., 2021). In particular, although there is only one other species of insectivorous bat on the island (*Taphozous mauritianus*, É. Geoffroy, 1818), it appears that this species can also be attracted to light sources, particularly those in stadiums (Barataud and Giosa, 2013), with potential new competitive interactions that remain to be studied. ALAN may also impact interactions between bats and their predators near light sources, although this should not be the case here, as there are no known aerial predators of bats on the island. Bat species whose abundance increases near lamps can experience barrier effects to movement, and thus a reduction of landscape connectivity, due to ALAN (Barré et al., 2023, 2021; Hale et al., 2015). Finally, although this remains to be studied, in particular for bats that can forage locally near lights, ALAN can also impact the physiology of bats with consequences that are still difficult to predict on their survival and reproduction (Boldogh et al., 2007; Cravens and Boyles, 2019). Therefore, in the light of previously acquired knowledge, positive phototaxis should be regarded as a disturbance to bat activity that should be mitigated.

### 4.2. *Light-induced changes in activity rhythms*

In terms of activity rhythms, regardless of lighting conditions, activity followed a bimodal pattern with peaks at the beginning and the end of the night. In Europe, such activity rhythms have been shown to be characteristic of insectivorous open and edge-space foraging species, which probably follow the peaks of insect emergence (Mariton et al., 2023). During the before period, the first peak in activity has the greater amplitude, whereas the second peak is more important during the after period. This reversal is observed both for control and treatment sites, suggesting that it is not related to the change in lighting conditions but



(A) After - Late - Precipitation x Site type

(B) Site type x Precipitation

(C) After - Core - Precipitation x Site type

(D) Site type x Precipitation

(E) After - Core - Precipitation x Dist. to light

(F) Dist. to light x Precipitation

**Fig. 5.** Predicted number of bat passes from GLMM during the after period according to the precipitation and the type of site during the late part of the night (A-B) and during the core part of the night (C-D); according to the precipitation and the distance to the nearest streetlight during the core part of the night (E-F). 95% confidence intervals are used. In (E), the confidence interval for 600 m was truncated for readability.

rather to other environmental conditions, perhaps, for instance, the higher average rainfall at the beginning of the nights during the after period.

The only effect of ALAN on activity rhythm was detected before the modification of the switch-off times, during the first half of the night. We found that the heavier the rainfall, the earlier the median time of activity at lit sites, whereas rainfall had almost no effect on the median time of activity at unlit sites. As complex as this result might be to explain, especially without information on light intensity and ambient light levels – which should be taken into account in future studies when appropriate equipment is available – they show that the effect of the presence of light is not neutral for bat activity rhythm and that it can interact with other factors. This is consistent with the few other studies showing that even the activity rhythm of apparently light-tolerant European species can be altered by ALAN (Hermans et al., 2024; Mariton et al., 2022). However, the mechanisms behind these changes in the activity rhythms of opportunistic bats due to light pollution remain to be studied, in particular to assess whether such alterations have an impact on individual fitness and population dynamics.

### *4.3. Effects of extending the PNL scheme*

After the implementation of the adapted PNL, the attractive effect of ALAN at the end of the night was still observed. Although bat activity likely reaches similar low levels regardless of the presence of ALAN when rainfall was heavy, as long as it remained moderate, bat activity was still higher at lit sites. This can be explained by the fact that the switch-on times in the second half of the night remained fairly similar between the before and after periods, hence the persistence of this impact. It could therefore be preferable to turn the lights back on later in the morning to allow more of the second activity peak to occur during the arranged period of darkness.

On the contrary, the effects of ALAN on activity levels and rhythms at the beginning of the night were no longer observed at lit sites. This shows that switching off the lights about two hours earlier – and thus allowing at least part of the first activity peak to occur during the arranged period of darkness – can effectively mitigate the effect of light pollution on this endemic species, unlike the initial switch-off times.

These results are consistent with the study of Azam et al. (2015), which showed that only late-emerging species may benefit from PNL if switch-off times are too late and reinforce calls by Day et al. (2015) and Mariton et al. (2023) for a better consideration of bat activity rhythm in the design of PNL schemes. Given that the activity rhythms of bats are likely linked to those of their prey, such bat-friendly PNL schemes could also help preserve the insect populations on which they feed. It would also be interesting to evaluate effectiveness of PNL schemes at other times of the year, such as during reproduction. This is all the more important as this measure could benefit the other bat species on the island as well as other taxa (both diurnal and nocturnal), such as seabirds nesting in the island, which would ideally need a PNL scheme all year round (Chevillon et al., 2022).

### *4.4. Implications and recommendations*

This study provides a novel empirical foundation at the local scale to support PNL – when designed to take into account species activity rhythms – as a biodiversity-friendly mitigation strategy. In particular, our findings show that *M. francoismoutoui*, the island's only endemic terrestrial mammal, responds to ALAN and that advancing switch-off times mitigates and even eliminates perturbations in the evening. Our results thus confer strong local conservation value and support extended PNL (*i.e*, switching off lights at 09:00 pm and, where feasible, switching them later in the morning) as a concrete, immediately achievable measure for this species. It highlights the relevance of PNL in insular settings, where range-restricted species are particularly vulnerable to increasing anthropogenic pressures. Our results shift the debate on PNL from a general precautionary approach toward an evidence-based demonstration, grounded in the environmental realities of the territory. These findings can strengthen the legitimacy of local public initiatives (which are often hesitant or subject to fluctuations in municipal political decisions) and enhance the advocacy capacity of on-the-ground actors, who often face political reluctance or conflicting demands (related to safety, tourism, or social expectations). In this context, identifying a coordinating actor emerges as a key issue to structure, mutualise, and amplify existing initiatives. The Réunion National Park could play such a role by bringing together municipalities, NGOs, state agencies, and scientists around a permanent coordination framework facilitating the alignment of actions across the island while respecting the ecological and socio-spatial specificities of each territory.

These findings also justify the integration of PNL into territorial planning documents and sustainable development policies. For instance, PNL could be formalised as a targeted measure in the Territorial Coherence Schemes (SCoT) or in the charter of the Réunion National Park, with explicit requirements for programming switch-off times that are compatible with the activity rhythms of species to be preserved. It could also be included as a priority environmental criterion in the specifications for public lighting development or renovation tenders. Such institutionalisation would help stabilise practices over time, beyond changes in local political leadership, and embed PNL in a more coherent territorial logic. The long-term effectiveness of these measures will also depend on their acceptance by the populations. Decisions on public lighting affect sensitive aspects such as comfort, safety, and nighttime uses, and cannot be addressed solely based on ecological expertise. Therefore, involving local residents in decision-making processes is essential to ground these policies in social realities and enhance their legitimacy.

The possible convergence of PNL benefits across different species opens the door to a broader territorial strategy. This calls for the mapping of priority zones for PNL, through the integration of species occurrence data, lighting infrastructures, new datasets on light pressure trajectories and the social uses of nocturnal space. This could lead to the establishment of a "*network of ecological actions*" for nocturnal environment preservation at the island scale and the development of new investigations that integrate species–habitat–infrastructure–use interactions. This perspective resonates with emerging reflections on dark ecological networks, which advocate for a socio-ecosystemic and territorially grounded approach to nocturnal environmental conservation (Challéat et al., 2021).

The different effects of PNL observed according to the time of night and weather conditions (notably precipitation) suggest that programming fixed switch-off times may be sub-optimal in some contexts. It opens a forward-looking avenue for adaptive lighting schedules informed by environmental variables (*e.g.*, season, rainfall) and expected activity peaks of sensitive species. This opens up possibilities for lighting management systems integrating such parameters into dynamic decision-making processes, and even for developing alert mechanisms or predictive regulation tools. This is one of the focuses of the CNRS Nocturnal Environment Observatory (https://observatoire-environnement-nocturne.cnrs.fr/en/) on Réunion Island, which operates a dense and long-term photometric sensor network (Challéat et al., 2023; Renaud et al., 2025). This system enables high-resolution spatiotemporal monitoring of light pressure and provides essential data for building models to understand and anticipate ALAN diffusion on the island's, including its variability with cloud cover and cloud-base height, which can strongly modulate nocturnal ambient brightness.

## CRediT authorship contribution statement

**Kévin Barré:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Léa Mariton:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Sarah Fourasté:** Methodology. **Laurent Godet:** Writing – review & editing. **Johan Milian:** Writing – review & editing. **Gildas Monnier:** Writing – review & editing, Methodology. **Matthieu Renaud:** Writing – review & editing. **Lisa Thiriet:** Methodology. **Samuel Challéat:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

## Acknowledgments

This work was supported by the Réunion National Park through the FENOIR program (*Figurations de l'environnement nocturne des territoires* *réunionnais*). We are also grateful to the municipality of Saint-Joseph, particularly its technical services, for providing public lighting data and valuable information on lighting schedules and PNL schemes. We thank UMR GÉODE for supplying the bioacoustic equipment and supporting the funding of the field mission. We also acknowledge UAR BBEES, CC-IN2P3, and PCIA-MNHN for providing the computing and storage facilities used to process the data, and Didier Bas for his assistance in this process. We also thank the two anonymous reviewers for their insightful comments on the manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111797.

## Data availability

The data used in this study can be found online at https://zenodo.org/records/18407498

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