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The rise of light-emitting diodes: do different colours of artificial light at night matter for bat disturbance?

Contents

Abstract

Artificial light at night (ALAN) is an increasing problem for wildlife. ALAN can have detrimental effects on physiological processes and other factors in animals. One group of species that is particularly affected by ALAN are the bats (*Chiroptera*). Predictions are that the amount of ALAN will grow with 6% each year. However, recent innovations have given rise to the LED lamps. These lamps are much more energy efficient, but can also be adjusted to virtually any colour. Studies indicate that light disturbance varies between colours, making the rise of LED light an opportunity to mitigate the negative effects of ALAN. Two additional important factors concerning the effect of ALAN on bats are the fact that light can function as a barrier and the mitigating effect of tree cover. The question that rises is what the exact effect of light colours is on bats and what the role of tree cover and the barrier effect are.

To answer this question, a literature review was conducted on this topic. Various results of studies on the effect of light colours and LED were compared in an attempt to find an answer to these questions.

In general, LED lamps seem to be less disturbing than conventional lamps and light of shorter wavelengths (white/green) seems to be more disturbing than light of longer wavelengths (red/amber). However, dark areas are always preferred over illuminated areas.

Tree cover can mediate the effect of ALAN in the form of a natural cover for ALAN. Results on the topic of light as a barrier are not consistent and more research is needed to explore this topic.

More studies need to be done on this topic, but LED lamps have the potential to reduce the negative effect of ALAN, especially when they are on the longer wavelengths. Also tree cover needs to be maintained and stimulated as much as possible to mitigate the negative effects of ALAN.

Introduction

Increasing levels of artificial light at night

Artificial light at night (ALAN) is an increasing worldwide problem for wildlife. Research has shown that the amount of artificial light has increased with 6% (0-20%) per year over the past decades depending on the geographic location (Hölker, 2010). This trend is expected to continue in the future. Increasing economic growth and urbanization comes along with an increase in an illuminated environment by humans. Lengthening of the anthropological day by artificial light is a result of the need for illuminated environments for humans because of safety, pleasantness and commercial purposes. Falchi et al (2016) conducted an extensive study on the amount of ALAN there is in the world now. They conclude that more than 80% of the world population lives in light polluted areas and more than one-third of the world population is not even able to see the milky way (Figure 1). They also conclude that differences are large between areas. Especially Europe and northern America are specifically light polluted, this can also be clearly seen in figure 1.

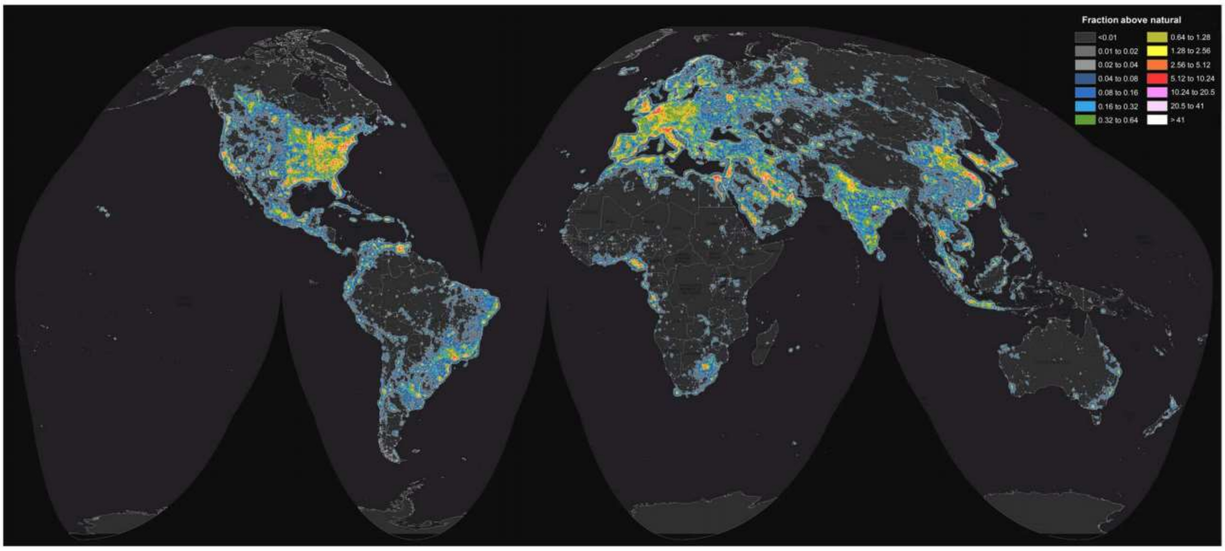

Figure 1 Overview of the current worldwide light pollution as computed by Falchi et al. (2016)

Light source innovation

Over the past decennia, the most commonly used types of artificial light source are the high-intensity discharge lamps such as MV (mercury vapour) and HPS (high pressure sodium). These lamps are used in all various outdoor environments such as street, parking lots and around buildings. These lamps tend to be very energy inefficient and are not manageable when it comes to colour (Energy.gov). The colour of these lights are generally full spectrum with peaks of intensity around green, blue and UV wavelengths (DiLaura & Houser, 2011).

In 2010, over 80% of the global artificial outdoor light sources were of these types, but over de past ten years the rise of the light emitting diodes (LED) has been tremendous. This type of light source is very energy efficient, meaning that more energy is used to produce light instead of heat such as in older light source types (Figure 2). It is also possible to alter the colour easily in various ways. In 2010, 4% of newly installed lamps were of the LED type, but in 2020 this number has risen to more than 60%. The prediction is that in the future this number will be even higher (Baumgartner, 2012).

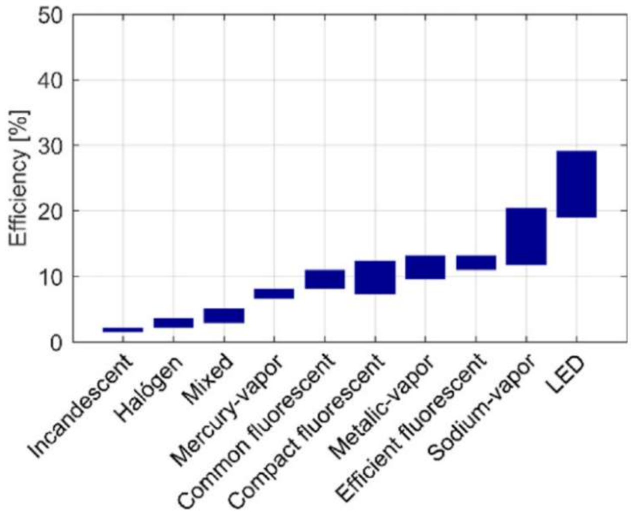

Figure 2 Efficiency of various light source types (DiLaura & Houser, 2011)

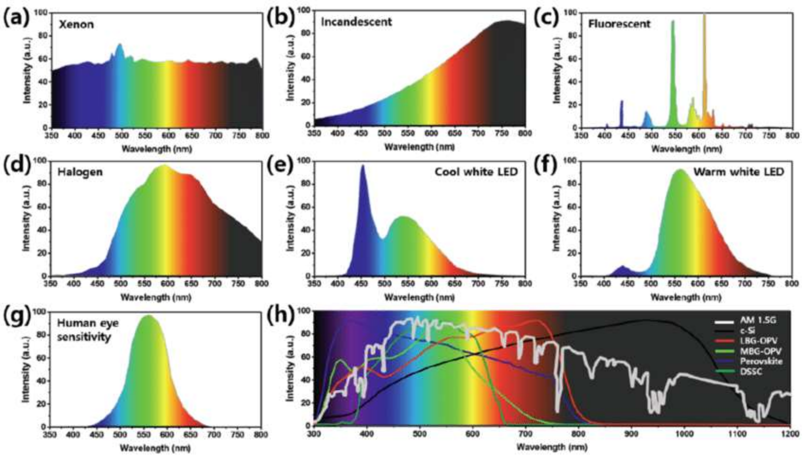

Figure 3 Light spectra for various types of light sources. Traditional lamps (b,c,d) have uncontrollable light spectra emitting very low and very high (UV) light. LED lamps can be managed in any way to only generate light at the desired wavelengths (Kim, 2019).

Effect of ALAN on wildlife

The increasing levels of ALAN can have negative effects on wildlife. Most organisms have evolved a molecular circadian clock which is managed by day and night-time light cycles (Hölker, 2010). These clocks are important for many physiological and behavioural aspects of the organisms. Sleeping rhythms for example are pre-dominantly managed by light dark cycles. Disruptions in these rhythms can have detrimental effects on the health of organisms with circadian clocks (Touitou, 2017).

Some species have evolved a special relationship with circadian light dark periods in form of becoming nocturnal. Nocturnal species are, in contrast to diurnal species, night active. This phenomenon is called nocturnality. Nocturnality has probably primarily evolved because of the reduced predation risk (Speakman, 1995). Being active in the night reduces the risk of being predated by other animals that mainly use visual sight for hunting or foraging. Nocturnality is therefore an important property of these species and is currently threatened by the unforeseen implications of the now widespread use of ALAN.

One important group of nocturnal organisms are the bats (*Chiroptera*). This group of Mammalia is important because it is one of the most diversified groups when it comes to species. Only the group of rodents (*Rodentia)* has more species worldwide (Voigt, 2011). Bats are important species because they are on a high trophic level in the food chain. They are important indicators for ecological changes in the environment, as Jones et al (2009) explained: ''*In particular, changes in bat numbers or activity can be related to climate change (including extremes of drought, heat, cold and precipitation, cyclones and sea level rise), deterioration of water quality, agricultural intensification, loss and fragmentation of forests, fatalities at wind turbines, disease, pesticide use and overhunting.''* Bats can thus be seen as an important taxon of species for the ecological environment, so research on bats is important to better understand the effects of environmental changes.

When it comes to environmental changes, especially light pollution can have detrimental effects on bats, because they have evolved to forage in dark environments (Voigt, 2011). According to Bradbury & Nottebohm (1969), in a research concerning *Myotis lucifug*us, high levels of light illuminance would impair flight orientation as bats would collide more often with obstacles when treated with high illuminance levels. This is probably because bats also use pattern vision in addition to echolocation, which disfunctions when illuminance levels are unnaturally high. In addition to this, Jones et al. (1994) concluded from field observations that *Myotis nattereri* avoid streetlights.
In contrast, reviews from other research on species of bats from the genera *Eptesicus, Nyctalus, Pipistrellus* and *Vespertilio* tell us that these species are rather light tolerant. These are all fast-flying aerial hawking species that forage on insects flying in the air (Lewanzik & Voigt, 2017). As also Gaisler et al. (1998) emphasize, these species might actually benefit from light pollution because insects generally concentrate around light sources during the night. Bats can then easily forage on these insects and be more efficient than foraging in ''normal'' darker areas. One question here is whether bats are attracted by the higher insect densities or that they show phototaxis independently from this. One important condition hereby is that these bats should be light-tolerant when it comes to for example flight orientation. As stated before, *Myotis* species are not light tolerant and might therefore avoid artificial light in contrast to the other mentioned genera. The fact that fast flying bats respond differently to ALAN than slow flying bats is probably because fast flying bats are more agile and have a smaller chance to be predated when flying in the light.

Complementary to the disruption of orientation in space as explained above, bats can also be disrupted in their orientation in time, as Fálcon (2020) mentions. The light dark cycle is one of the most important inputs for the circadian clock in many organisms. Many physiological systems including sleep-wake cycles are managed by light. Artificial light can disrupt this cycle, because there can be light at unnatural moments. What the effect of artificial light exactly means for sleep-wake cycles in bats is still unknown.

Another impact of ALAN on bat populations is that light can function as a barrier. Long transects of artificial light along roads and other structures can fragmentate foraging ground and obstruct migration and commuting routes (Altringham & Kerth, 2016). Especially woodland adapted and slow flying species can be affected by this.

An important factor for disturbance by ALAN is the light intensity. But Pauers et al. (2012) showed that not just the intensity, but also the wavelength of the light is important for disturbance in the circadian clock. This means that the colour of the light is an important factor in the amount of disturbance it generates. Some research has been done on what light colours exactly mean for disturbance in bats, but not much. One reason for this is that the possibility to alter the light colour of artificial light is relatively recent.

Effect of light source innovation on bats

With the rise of LED-lamps come great applications and anthropological purposes, as stated above, LED lamps are not just much more energy efficient, they can also be adjusted to have virtually any colour. This is possible, because of the new, more modern way these lamps are made (Gilman, 2013). Bats can benefit from the new possibility to modulate the colour of ALAN, because it is now possible to exclude light of higher wavelengths (blue/white light) from the artificial light. Already, you can see different colours of light being used in the wild in an attempt to not disturb bats and other wildlife, but still create the safety and pleasantness humans demand from some areas. There is however not yet a clear understanding of the different effects of colours on the behaviour of bats and other wildlife. To implement the right colour with the aim to create the least disturbance, it is important to first research this topic and compare the multiple findings.

Tree cover as a mediating factor

Multiple studies teach us that tree cover is an important mediating factor when it comes to light disturbance in bats (Stone et al., 2015; Rowse et al., 2016). Bats often seek refuge under tree cover when ALAN is present. Tree cover may mitigate the disturbance of ALAN on migrating bats. It can also mitigate the potential negative effect of ALAN on urban habitat destruction. It is however not clear what the effect of the new LED lights and colour differences is on bats. Also the differences between species are still largely unknown.

Research question and aim

To investigate the possible effects of ALAN on bat populations, I will conduct a literature review on various articles about the effect of ALAN on bat behaviour to better understand the implication of ALAN on bat populations. I will especially focus on the effect of different colours of light, because, as mentioned before, recent technological innovations have made it possible to vary light colours because of the rise of LED street lighting. The effect of different colours of light is not fully understood yet. The research question formulated for this review is ''*What is (known about) the effect of different light-colours on the behaviour of bats?''* Additionally, to study the effect of tree cover the sub question ''*How can tree cover mitigate the potential negative effect of ALAN?''* was formulated and to study the potential effect of light as a barrier the sub question *''Can light function as a barrier and what is the importance of colour?''.*

There are two main players in the field of research on light disturbance in bats. One is Kamiel Spoelstra (Department of Animal Ecology, Netherlands Institute of Ecology in Wageningen) and the other one is Christian Voigt (Department of Evolutionary Ecology, Berlin). Both research groups have conducted multiple experiments about the effect of light pollution of different colours on the behaviour of bats. The outcomes are not always consistent and therefore it can be worthy to collect and compare the various findings.

Research review

Effect of LED transition

First it is important to understand what the effect of the transition from conventional light to LED light might mean for bats. Lewanzik & Voigt (2017) made an attempt to investigate this. In their paper the aim is to identify the effect of the transition from conventional street lighting to LED on the activity of urban bats. They distinguished 5 (groups of) species: *P. pipistrellus*, NEV group (Genera *Nyctalus Eptesicus and Vespertilio*), *P. nathusii*, *P. pygmaeus* and *Myotis Spp*. The genera *Nyctalus Eptesicus and Vespertilio* are taken together, because these species have a similar ecology.
In the experiment they recorded all bat-calls around 46 conventional lamps in 2011. They then replaced 25 of the 46 lamps by modern LED lamps and compared the results. They do not specify the colour of the newly installed LED lamps but do state that the LED lamps send out much less UV light than the traditional lamps.
They found different results for different species. Activity by *P. pipistrellus* decreased by approximately 50% when LED lamps were installed. Probably because LED lamps induce less phototaxis for flying insects. For the NEV group, *P. nathusii* and *P. pygmaeus* no significant effects of replacing the lamps were found. The interaction between year and treatment did not show a significant result. In contrast, for the *Myotis* group which is considered to be light averse a significant effect was seen. Activity decreased for the control/conventional lamps circumstances, but did not change for the LED treatment. In figure 4, the bottom right graph also shows this exceptional result for the *Myotis* group.
They conclude that light tolerant bat species as *Pipistrellus* and the NEV group are either indifferent on flying near conventional light sources or LED lamps (NEV group) or reduce their activity near LED lamps, because LED lamps attract fewer flying insects than conventional MV lights. Light averse species as *Myotis spp.* relatively increase their activity when conventional lamps were replaced by LED lamps, probably because LED lamps emit less UV light which is considered to be the most disturbing part of the light spectrum for *Myotis spp.* (Jones et al., 1994). They conclude that replacement of conventional lamps by LED lamps could increase the activity of *Myotis spp.* by 4-5 fold.

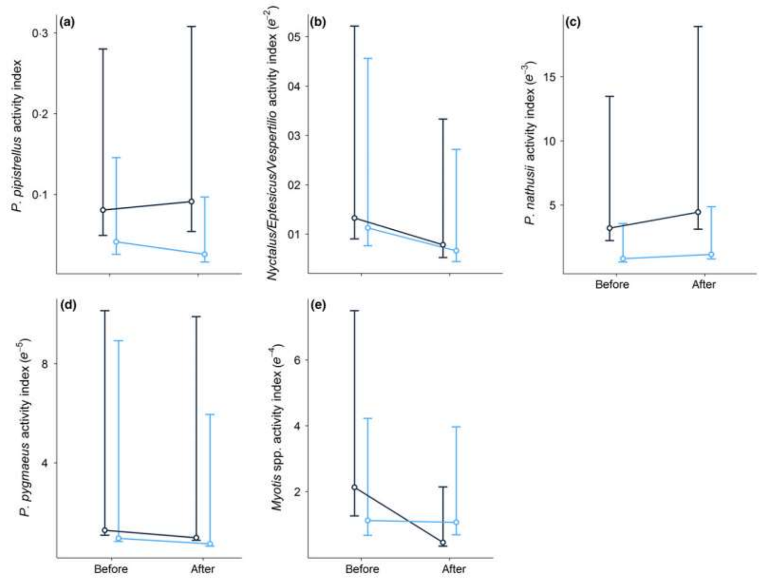

Figure 4 Activity indices of five bat species (groups) that were recorded at urban street lights both before and after high-pressure mercury vapour (MV) illuminants of experimental lights (light blue) were replaced by light-emitting diodes, while control lamps (black) remained MV lamps throughout the entire study. Depicted are model predictions (dots) and 95% credible intervals (error bars).

Light as a barrier

As mentioned in the introduction, light can also be a barrier for some bat species with the result of fragmentation of habitats. The effect of LED lights on this potential negative effect is an important subject and the potential to manage this negative effect by altering the colour is a great opportunity.

Straka et al. (2020) try to investigate the effect of different colours of LED light on cave bats in Bulgaria, which will be specified later. The paper consists of two experiment, one lab experiment mimicking a cave environment named ''Flight room experiment'' and one field experiment near the entrance of a cave named ''*Cave entrance experiment*''. The species selected for the experiments are *Miniopterus schreibersii* and *Myotis capaccinii* for the flight room experiment and *Rhinolophus euryale*, *R. mehelyi*, *M. schreibersii* and *M. capaccinii* for the cave entrance experiment. The light chosen for the experiments were LED light in the colours white (broad spectrum), red (630 nm) and amber (597 nm). The amber light is also called a "Bat light".

Flight room experiment

Both species were released in a room divided into 2 sections. Both sections were treated in all possible combinations of dark, white, red and amber colour. The preference of the bats was then calculated by quantifying the activity in both sections. The largest preference was found in the treatment where one section was illuminated with white light and the other section with red light. The preference was 55-60% for red light, concluding that red light gave the least disturbance. Results were consistent between both species.

Cave entrance experiment

The cave entrance experiment was set up by separating the entrance of the cave into 2 light-tight sections. Light treatments were than combined similar to the flight room experiment. In this way, bats leaving the cave were forced to choose between light treatments. The colour combinations were alternated in such a way that all combinations would be present.

As can be seen in figure 5 the results showed that all species avoided the light treated section when this was the left side. Only *Rhinolophus* spp. avoided both sides when lit. Differences between light colours were small, however red light (rd) shifted the activity slightly less than white and amber light (wd and ad).

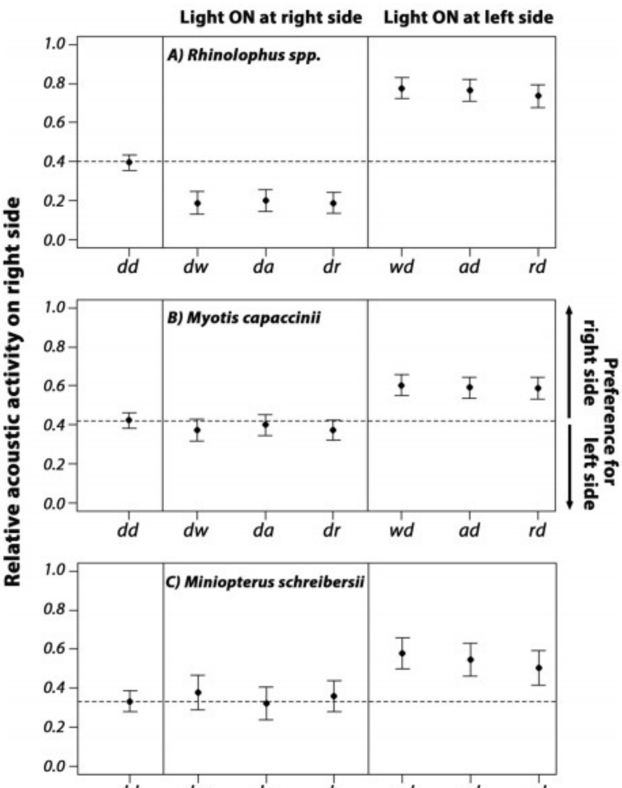

Figure 5 Predicted relative acoustic activity of Rhinolophus spp., M. capaccinii and M. schreibersii (estimate and SE) at the cave entrance during the dark-dark control (first box) and under different treatments of one-sided lighting (second box ¼ light on in the right compartment, third box ¼ light on in the left compartment, d ¼ dark, w ¼ white, a ¼ amber, r ¼ red). Predicted relative acoustic activity is expressed relative to the right compartment. First and second letter of the abbreviated treatment category code indicate the light at the left and right compartment, respectively. The dashed line indicates the relative acoustic activity in the right compartment under the dark-dark treatment. Values above the dashed line indicate a preference of the bats for the light on the right side, which is named second in the abbreviated treatment category, and values below the dashed line indicate a preference for the light on the left side. (Straka et al., 2020)

Straka et al. conclude that all colours of LED light disturb the selected bats with *Rhinolophus spp.* being the most light averse. Red light was in general the least disturbing and they propose that this colour should be selected for illuminating areas with bats. Red light is however still disturbing and dark areas must be maintained.

Another study on the effect of LED lights and light colour on commuting bats is a study by Spoelstra et al. (2018) on *Myotis daubentonii*, a choice experiment was set up to investigate whether this species would prefer light of different colours when commuting through a culvert. Over multiple nights, 2 culverts where the bats fly through were enlightened with green, red and white light. The activity in the culverts was then measured to determine the preference of the bats. They found no significant effect of any light treatment on the choice of the bats (Figure 6).

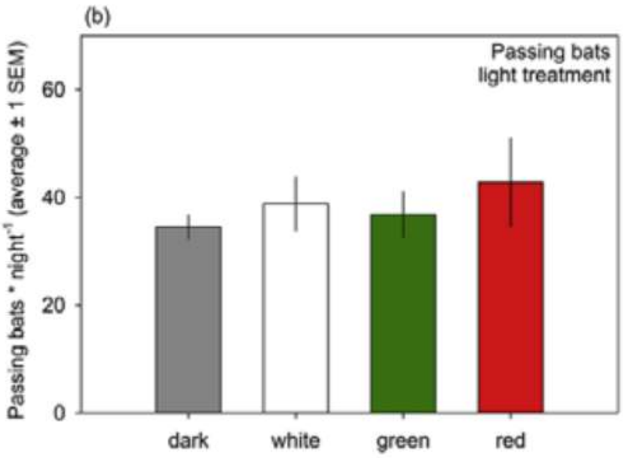

Figure 6 Number of passing M. daubentonii for each light treatment. (Spoelstra et al., 2018)

The effect of light colour

To answer the question what the effect of different colours is on foraging and migrating behaviour of bats, I will look at some studies that investigated this.

Voigt et al. (2018) investigated the phototaxis of the Nyctaloid group, *P. nathusii* and *P. pygmaeus.* They used LED lamps in the colours red (631 nm) and warm-white (576 nm). They investigated this by conducting a field study where they put up poles in the field with lamps of the different colours. They distinguished three areas: landside, central and seaside.
They found that *P. nathusii* and *P. pygmaeus* increased activity near red LED lamps, they could not show this trend for the Nyctaloid group. For the warm-white treatment, they only found an increase in activity for *P. nathusii* when the lamp was put up near the landside. They did not record an increase in feeding activity near red lamps, but did find an effect for the warm-white lamps for *P. nathusii.*
This study shows that red light attracts *Pipistrellus sp.* and on the landside white light attracts *P. nathusii.* No effect is seen for other species.

Spoelstra et al. (2017) conducted a field experiment near a forest edge to study the effect of different colours of light on bats. They included three groups of species: *Myotis sp. + Plecotus sp., Pipistrellus sp.* and *Nyctalus sp. + Epseticus sp.* They installed 4 transects consisting of 5 poles perpendicular to a forest edge (Figure 7). The lights were turned on during the night and the activity of the bats was measured.

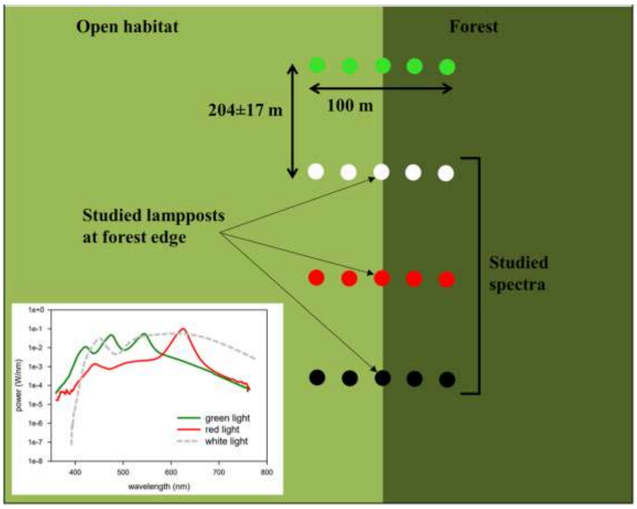

Figure 7 Overview of the experimental set up (Barré et al. 2021)

For *Pipistrellus sp.* they found that activity increased along the transects for white light and in green light. No effect was seen for red light. For *Nyctalus sp. + Epseticus sp.* a large increase was seen for green light and a slight increase for white light. For *Myotis sp. + Plecotus sp,* compared to the dark transect, a large decrease of activity was seen for white and green treatments, but no effect was seen for red treatment (Figure 8).
They conclude that *Pipistrellus sp.* and *Nyctalus sp. + Epseticus sp.* exploit the increase of insects near green and white lamps. They are able to do this because these species are more agile and can avoid predation because of this. In contract, *Myotis sp. + Plecotus sp.* are much less agile and avoid green and white light, because of the increased predation risk.

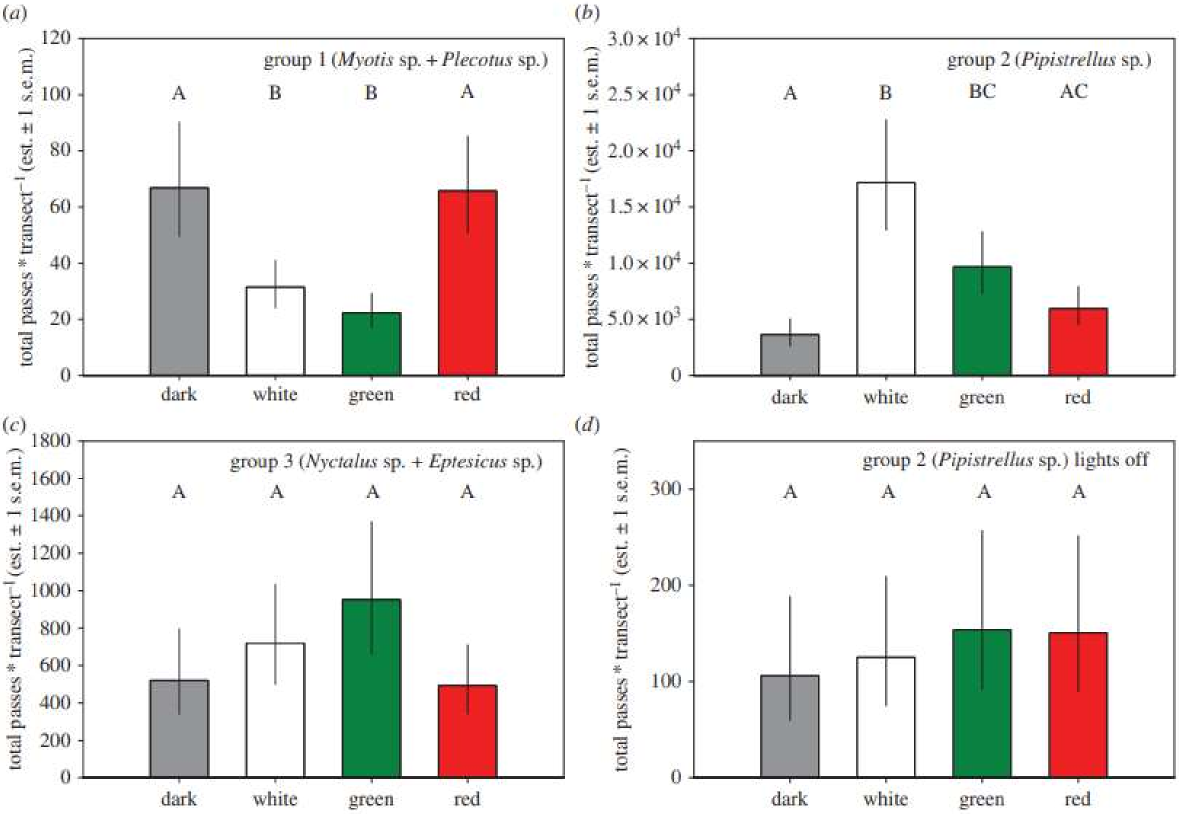

Figure 8 Total bat passes (summed over all nights measured per transect) during all years 2012 – 2016 (back-transformed treatment estimates from negative binomial generalized linear models with bat passes and site as fixed effects) for (a) group 1 (Myotis and Plecotus species), (b) group 2 (Pipistrellus species), (c) group 3 (Nyctalus and Eptesicus species) and (d) passes of group 2 bats during nights when the lights were off for moth sampling (electronic supplementary material, table S2). Capitals identify groups that significantly differ from each other in post hoc tests (electronic supplementary material, table S3). (Spoelstra et al., 2017)

In an attempt to clarify the potential fitness effects of ALAN, Spoelstra et al. (2015) propose that ALAN can directly and indirectly effect population fitness of bat species (Figure 9). They say that ALAN can directly influence fitness of specific individuals, but that the total effect of ALAN is much more complicated, because of the cascading effects ALAN has on the environment, physiology, behaviour and life-history choices of bats. For example, ALAN can lead to untimely reproduction, lowering fitness of offspring and thus leading to population decrease. ALAN can also drastically change the environment of the bats by for example decreasing prey densities.

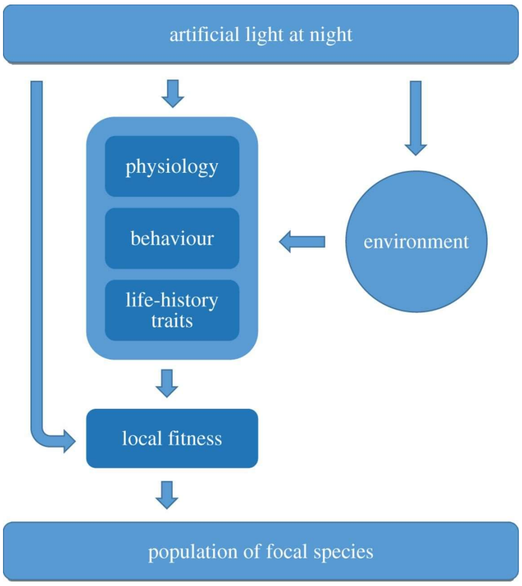

Figure 9 Flowchart of fitness effects of ALAN on bat species (Spoelstra et al. 2015)

To investigate the effect of ALAN on fitness Spoelstra et al. (2015) conducted an experimental field study to investigate the effect of ALAN on free living bats. They used the same set-up as Spoelstra (2017). Overall, activity of *Pipistrellus spp.* was much higher along the green transect and slightly higher around the white transect, no effect was seen for the red treatment. (Figure 10).

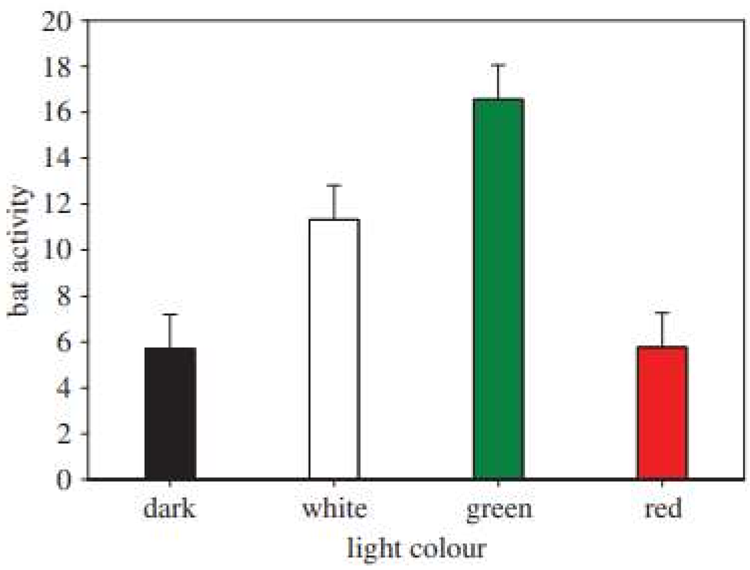

Figure 10 Common pipistrelle (Pipistrellus pipistrellus) activity represented by the number of call sequences per night per transect (model estimates for light treatment corrected for random variables). Error bars indicate standard error.(Spoelstra et al., 2015)

They also measured the amount of moths along each transect, but found no significant differences (Figure 11).
According to these results, *Pipistrellus spp.* are attracted by green and white LED lamps, but cannot take advantage of increased moth activity.

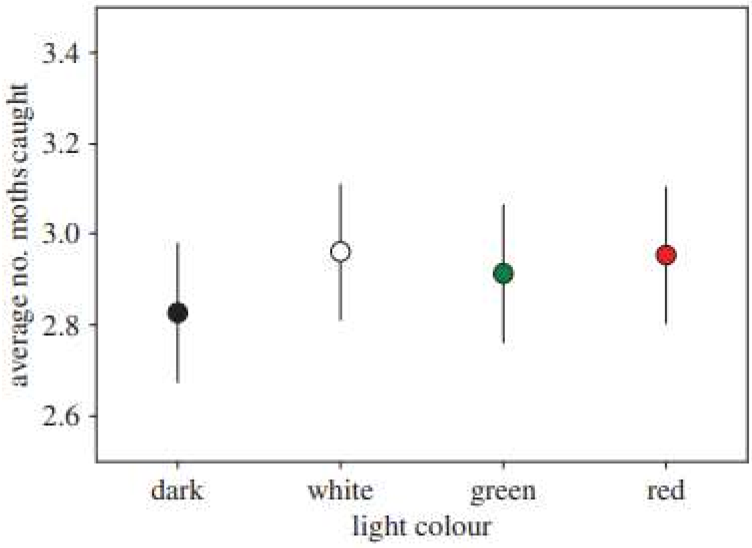

Figure 11 Average of the total number of moths caught per family (Erebidae, Geometridae, Noctuidae, Notodontidae and Sphingidae; model estimates for light treatment corrected for random variables) per light treatment per transect per night. Error bars indicate standard error.

Tree cover

Bats often forage and commute under and along tree lines. Previous studies showed that tree cover can potentially mitigate the negative effects of ALAN. Straka et al. (2019) try to investigate the role of LED light and colours on this interaction in their study on the effect of tree cover on light disturbance for traditional UV emitting lamps and modern LED lamps that do not emit UV light. The study consists of a field study with no experimental treatments. Multiple study sites around Berlin were selected with a variety of landscape. In these areas the lamps were quantified and categorized in UV emitting (MV and MH lamps) and non- UV emitting (LED lamps). Activity was then recorded in all areas and quantified to analyse the activity per area for alle species. They distinguish NEV group, *P. pipistrellus, P. nathusii, P. pygmaeus and Myotis spp.*

They found that the activity of both *P. pipistrellus* and *P. nathusii* increased with the number of UV emitting lamps. *P. Pygmaeus* Myotis spp. and the NEV group species reduced their activity with the number of UV emitting streetlamps. Concerning the non-UV-emitting LED lamps, activity of all species except *P. pygmaeus* decreased when there were more lamps. *P. pygmaeus* showed no response.

During the study they also looked at the interaction of tree cover and ALAN on bat activity. They found a positive interaction for *P. pipistrellus, P. pygmaeus* and *Myotis spp.* between tree cover and light disturbance of both UV and non-UV emitting lamps. No significant interaction was found for *P. nathusii* and a small positive interaction for the NEV group.

They conclude that in general, UV emitting lights disturb most species of bats and that these UV emitting lamps should be avoided. They also conclude that tree cover reduces the negative effects of ALAN, where tree cover remains important for bat habitat in urban environments.

To also investigate the effect of light colour, Barré et al. (2021) investigated the effect of tree cover on the spatial behaviour of bats, very much like Spoelstra et al (2015 and 2017). Three transects were placed perpendicular to a forest edge. One transect was equipped with white light, one with red light and one was left dark (Figure 12).

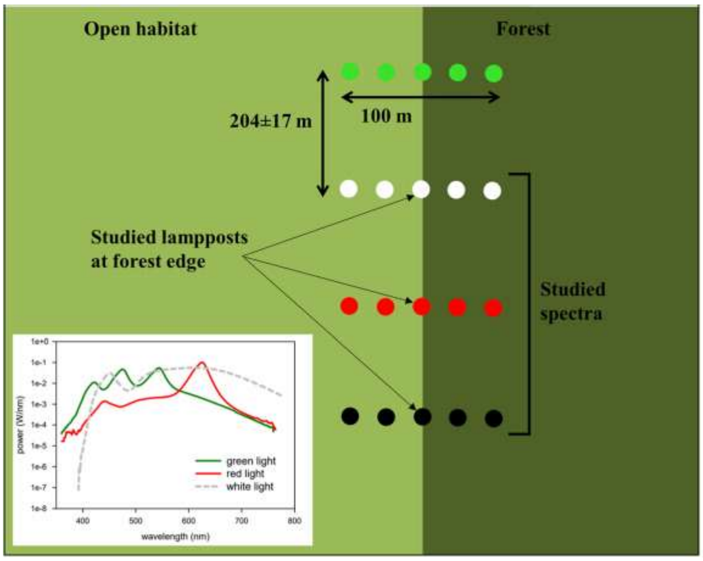

Figure 12 Overview of the experimental set up (Barré et al. 2021)

Via 3D visualization the position of the bats was determined and the effect of different colours of ALAN was calculated. They included three groups of species in the experiment: *Myotis sp./Plecotus sp., Pipistrellus sp.* and *Nyctalus sp./Epseticus sp.*

They measured the effect of light by calculating the probability of flying in the forest (PFIF), where a

higher PFIF corresponds with more disturbance.
For *Pipistrellus sp.* they found that the PFIF was higher when they flew around red and white lights, while only significantly higher for *Nyctalus sp./Epseticus sp. and Myotis sp./Plecotus sp.* when flying near white light (Figure 13). In the figure it can be clearly seen that white light treatment gives similar results between species, but only *Pipistrellus sp.* fly inside the forest under red light treatment. When flying three to five metres from a white light, *Nyctalus sp./Epseticus sp. and Myotis sp./Plecotus sp.* the PFIF was 100%, while this is only 1% in unlit areas. Similarly, the PFIF of *Pipistrellus sp.* reached 85-50% when flying 1 metre from white and red light.

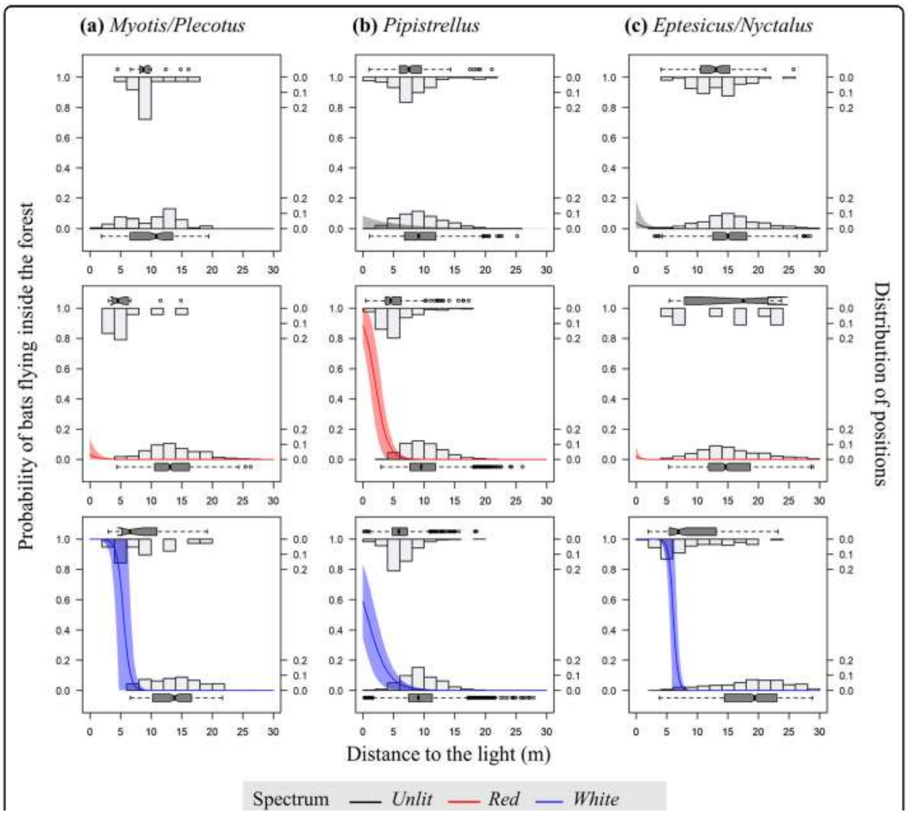

Figure 13 Results of Barré et al. (2021) on the PFIF for different light treatments.

Discussion of different findings

Overall, all studies find results that sometimes match and sometimes do not match. In general, all find that genera of bats that are commonly considered light averse, such as species from the genera *Myotis and Plecotus* in fact do avoid light of each type and colour and species that are considered light tolerant (*Pipistrellus* and the genera *Nyctalus, Eptesicus and Vespertilio)* are attracted or not affected by light.

<u>The effect of LED innovation</u>

The only paper discussed that studied the effect of the change from conventional lights to LED lights is the paper by Lewanzik & Voigt (2017). For this reason this paper is especially valuable. They find that light tolerant species decrease their activity when LED lamps are installed and explain these by the assumption that LED lamps attract less insects than conventional lamps, they did however not measure this in the study. Measuring the change in food availability would be a very valuable addition for this study. Especially, because Spoelstra et al. (2015) did measure the insect availability in their study in the form of moth counts. They found a significantly higher activity of the light tolerant species *Pipistrellus sp.* near white and green LED light compared to the dark control area, but did not measure a difference in moths quantity. The question here is whether only counting moths in the study area is a good measure of insect activity, this is important because *Pipistrellus sp.* predate a great variety of insects. The fact that Lewanzik & Voigt (2017) do not mention the colour of the LED lights they used makes it difficult to use the results of Spoelstra (2015) to explain the results of Lewanzik & Voigt (2017). If however insect activity did not increase under green and white LED light, but *Pipistrellus sp.* activity did, the increase of activity might not be because of a higher insect density, but because of phototaxis of *Pipistrellus sp.* This would mean *Pipistrellus sp.* cannot take advantage of increased foraging efficiency but have a greater thread of being predated. The lack of information about insect densities and quantities in these studies greatly reduces the information of fitness effects that can be learned.

<u>The effect of light colour</u>

The colour of the light seems to matter when it comes to light disturbance in bats (Figure 8, 10 and 13). Results of different studies are however not consistent. Voigt et al. (2018) find that the only species affected by light is *Pipistrellus spp..* These species are attracted by red light and only *P. nathusii* by white light on the landside. This is a large contrast when compared to Spoelstra et al. (2015 and 2017), who find that *Pipistrellus spp.* are not affected at all by red light compared to dark treatment, but are affected by green and white light. Spoelstra et al. (2015) find a higher effect of green light and Spoelstra (2017) find a higher effect of white light.
When it comes to the light averse species such as *Myotis spp.* the results of Spoelstra et al. (2017) show a large decrease of activity for green and white light and no effect for red light, compared to dark treatment. In contrast, Voigt et al. (2018) did not find an effect.
When it comes to the *Nyctalus & Eptesicus* species, Spoelstra et al. (2017) find similar effects as for *Pipistrellus sp.*, which is not surprising, because they both belong to agile and fast flying bats.

Considering fitness effects, except for Spoelstra et al. (2015), the papers discussed in this review do not mention the fitness effects of the found results. In the end, the effect of ALAN on the fitness of bat species is the most important, therefore the lack of attention for this aspect in most papers is unfortunate.

<u>Light as a barrier</u>

When comparing the choice experiments of Straka (2020) and Spoelstra (2018) on *Myotis spp.* and *Miniopterus schreibersii,* Spoelstra et al. did not find any significant results. This research however

comes with some reservations. As they also acknowledge, the lamps used in this paper were installed inside of the culverts where the bats commute through, which means the bats only encountered the light after they made the choice for the two culverts.
Straka et al. did find significant results for both *M. capaccinii* and *M. schreibersii.* Both species avoid white, amber and red light equally when exiting a cave. In the laboratory experiment Straka et al. found that *M. capaccinii* and *M. schreibersii* had a strong preference for red light, when they were forced to choose between red and white light. This laboratory experiment could also be carried out by Spoelstra et al. (2018) on their study species *Myotis daubentonii.* This experiment eliminates the weaknesses of the field experiment by Spoelstra et al. and can give insight in the way *Myotis daubentonii* respond to light of different colours.

Tree cover

Considering the interaction of tree cover and ALAN, different studies find different results. Both Straka et al. (2019) and Barré et al. (2021) studied this interaction in a slightly different manner. Barré et al (2021) calculated the exact position of the bats on a forest edge, while Straka et al. (2019) used the GPS position of the bats to determine whether they were flying in open or tree-covered areas. Straka et al. (2019) found relatively more activity near tree cover for *Pipistrellus pipistrellus, Myotis spp.* and the NEV group, but not for *P. nathusii and P. pygmaeus* when exposed to LED light. In contrast, Barré et al (2021) found a higher possibility of flying inside the forest for all species (*Pipistrellus* group, *Eptesicus/Nyctalus* and *Myotis/Plecotus).* Results might have been different if Barré et al. studied the species of the *Pipistrellus* group separately.

Conclusion

The aim of this review was to find an answer to the question what the effect of the colour of ALAN is on the disturbance of bats. Recent innovations in the form of LED-lamps made it possible to easily alter the colour of light used in our environment. Various studies on this topic have been discussed. The effect of the transition from conventional light to LED light, the meaning of the different colours and the mitigating effect of tree cover have come forward. General findings suggest that LED lights in general are less disturbing than conventional lights and there is also a different effect of different colours. Results are however not consistent between species. The results of the discussed papers suggest that light tolerant species such as *Pipistrellus spp.* and species of the NEV group are indeed less influenced by ALAN. This is probably because they can fly faster and are more agile than species from the *Myotis* and *Plecotus* group, which are generally more disturbed by light.
When it comes to colours, shorter wavelengths (white/green) seem to be more disturbing than colours of longer wavelengths (red/amber), although results are not always consistent between studies.

When it comes to the topic of light functioning as a barrier, I can conclude that the discussed papers in this review do not give a definitive conclusion. Multiple studies find prove for light as a barrier near roads and other transects, but when it comes to light colour, more research is necessary.
Tree cover seems to mitigate the negative effects of ALAN. Bats seem to seek refuge under tree cover when they are affected by white light and for *Pipistrellus sp.* also by red light (Barré et al., 2021). Also, in areas affected by ALAN, bats are more active when there is tree cover (Straka et al., 2019). To mediate the effect of ALAN on bats, maintaining sufficient tree cover seems to have a positive effect.

An important question that remains unanswered is what the fitness consequences are of the observed effects of light. In most studies, disturbance is thought of as a deviation of normal, dark, environments. Some evidence shows that species as *Pipistrellus spp.* increase activity near artificial light sources, probably because of increased insect densities, this is however not always the case (Spoelstra et al., 2015). In these cases disturbance is not necessarily of bad influence on the fitness of these species. Other species as *Myotis spp.* that are considered light averse, because they have a higher threat of predation as a result of lower flying speeds avoid light sources of especially white and green colour (Spoelstra et al., 2017). *Myotis spp.* also increase activity when conventional light sources are replaced by LED lights relative to areas where conventional lamps were maintained (Straka et al., 2020). One possibility is that light tolerant species can take an advantage over light averse species, because they can exploit the potential high insect densities, while light averse species cannot and need to forage in less insect dense areas. This would mean ALAN would give light tolerant species a higher relative fitness. For ecological durability, species richness is very important so a good balance in fitness between species should be pursued.
For the conservation of diverse bat populations, good management of ALAN is important. For the least disturbance, dark environments are preferred and should be maintained as most as possible. When this is not possible, the negative effects of ALAN can be partially managed by adjusting the colour of the light to longer wavelengths. Most studies conclude that red light is the least disturbing and white light and UV light disturb the most. Therefore, as studies continue to find results, ALAN should be coloured red whenever possible to give the least disturbance when it comes to bats. In this advice the effect of red light on other wildlife is not considered and more research needs to be conducted to come to the optimal colour of ALAN.

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Appendix 1

Schematic overview of the papers discussed in this review. In the table the treatment, species and results are displayed per paper.

Paper	Treatment	Species	Effect
Lewanzik, Voigt 2017	MV->LED	*P. pipistrellus*	Activity↓
		NEV group	None
		P. nathusii	None
		P. pygmaeus	None
		Myotis spp.	Activity↑
Straka, Voigt 2020	Dark → LED red	*Rhinolophus spp.* *M. capaccinii* *Miniopterus schreibersii*	Activity↓
	Dark → LED amber		Activity↓↓
	Dark → LED white		Activity↓↓ ↓
Straka, Voigt 2019	UV ←→ Dark	*NEV group*	Activity↓
		P. pipistrellus	Activity↑
		P. nathusii	Activity↑
		P. pygmaeus	Activity↓
		Myotis spp.	Activity↓
	Dark ←→ LED (non-UV)	*NEV group*	None
		P. pipistrellus	Activity↓
		P. nathusii	Activity↓
		P. pygmaeus	None
		Myotis spp.	Activity↓
Voigt, 2018	LED-red	*P. nathusii*	Activity↑
		P. pygmaeus	Activity↑
		Nyctaloid	None
	LED-warm-white	*P. nathusii*	Activity↑
		P. pygmaeus	None
		Nyctaloid	None
Spoelstra, 2015	Dark → LED red	*Pipistrellus sp.*	None
	Dark → LED green		Activity↑
	Dark → LED white		Activity↑
Spoelstra, 2017	Dark → LED red	*Pipistrellus sp.*	None
		Myotis sp. + Plecotus sp	None
		Nyctalus sp. + Epseticus sp	None
	Dark → LED green	*Pipistrellus sp.*	Activity↑
		Myotis sp. + Plecotus sp	Activity↓
		Nyctalus sp. + Epseticus sp	Activity↑
	Dark → LED white	*Pipistrellus sp.*	Activity↑
		Myotis sp. + Plecotus sp	Activity↓
		Nyctalus sp. + Epseticus sp	Activity↑
Spoelstra, 2018	White	*Myotis daubentonii*	None

	Green		None
	Red		None
Barré, 2021	White	*Pipistrellus sp.*	Seeking refuge
		Myotis sp. + Plecotus sp	Seeking refuge
		Nyctalus sp. + Epseticus sp	Seeking refuge
	Red	*Pipistrellus sp.*	Seeking refuge
		Myotis sp. + Plecotus sp	Not significant
		Nyctalus sp. + Epseticus sp	Not significant