

Advantages and disadvantages of ALAN on several bat species in Europe.

Dide Hormes
s3812901

Bachelor's thesis
Faculty of science and engineering
Supervisor: Barbara Helm
July, 2021

Abstract

Artificial Light At Night (ALAN) has been a widespread phenomenon in the last decades, affecting bat species in different ways. The focus of this review is to determine which European bat species are most vulnerable to ALAN by using multiple studies on bat behaviour to identify advantages and disadvantages of ALAN. Based on their behaviour around ALAN the bat species can be classified into 4 groups, namely medium-sized fast-flying bats (*Nyctalus* and *Eptesicus* species); small fast-flying bats (*Pipistrellus* species); maneuverable slow-flying bats (*Myotis* and *Plecotus* species) and bats foraging above water (*Myotis daubentonii* and *M. dasycneme*). *Myotis* and *Plecotus* species are light-deterred. The cause is the increased predation risk around ALAN, which especially affects slow-flying species. Their light avoiding behaviour can lead to habitat fragmentation, less available roosting places, less available foraging places, less prey availability and a shorter activity period. *Nyctalus*, *Eptesicus* and *Pipistrellus* species are light-opportunistic species. They exploit the accumulation of insects around lights, which leads to an increased food intake. Lights attract insects from a distance, depleting the darker areas of these insects. This vacuum cleaner effect negatively influences *Myotis* and *Plecotus* species. In conclusion, light-opportunistic species experience the most advantages from ALAN, while light-deterred species experience mainly disadvantages. This could have implications for the bat species composition in illuminated areas.

Table of contents

Introduction	4
Effects of ALAN on predation	8
Effects of ALAN on foraging	9
Effects of ALAN on emergence time	12
Discussion	13
References	15

Introduction

Artificial Light At Night (ALAN) has been a widespread phenomenon in the last decades. It has been increasing since the 1950's to a point where 23% of the land surface of the planet experienced artificially elevated levels of night sky brightness (Owens et al., 2020). This affects mammals, birds, invertebrates, reptiles, amphibians, fish and plants (Rich & Longcore, 2006). It can influence circadian, circannual and circalunar rhythms, migration, physiology and all kinds of behaviour (Rich & Longcore, 2006). One example of animals that have been shown to be affected are bats. Bats are nocturnal animals, so they often encounter ALAN. Different bat species can have a different response to ALAN. For example, in one study *Pipistrellus species* increased in abundance at street lights, while *Myotis species* decreased in abundance at street lights (Spoelstra et al., 2017).

The question is whether one strategy exceeds the other, which would give that species an advantage in illuminated areas. The species most vulnerable to ALAN may decrease, while the species least vulnerable to ALAN may increase, influencing the species composition. The focus of this review is to determine which European bat species are most vulnerable to ALAN by identifying advantages and disadvantages of ALAN for different bat species.

Different bat species differ in size, flight speed, maneuverability and echolocation call characteristics. Subsequently this determines their diet, foraging technique and habitat use (Rydell, 2006). These differences are the reason for different responses to ALAN. Partly following the observations of Rydell (2006) the bat species can be classified into 4 groups based on their behaviour around ALAN. These groups will be referred to throughout the review.

The first group consists of species of medium-sized fast-flying (about 10–30 g) bats. Faster and larger bats are typically less maneuverable, therefore they forage in open areas in long straight lines (Rydell, 2006). They usually dive at their prey from height. The *Nyctalus* and *Eptesicus spp.* are represented in this group. They forage on somewhat larger flying insects. The diets and roosting places of these species differ (table 1). *Nyctalus spp.* roost in trees and often eat moths (Lepidoptera), beetles (Coleoptera), mosquitoes (Nematocera), flies (Diptera), caddisflies (Trichoptera) and net-winged insects (Neuroptera). *Eptesicus serotinus* roosts in buildings and mainly eats larger species such as moths (Lepidoptera) and beetles (Coleoptera).

The second group consists of smaller (less than 10 g) fast-flying bats. Smaller bats are more maneuverable (Rydell, 2006), so they are able to forage in semi-open environments. They forage typically on small flying insects. This group is represented by the *Pipistrellus spp.* *Pipistrellus pipistrellus* sleeps in buildings and eats all flying insects (table 1). The *Pipistrellus nathusii* sleeps in trees and mainly eats mosquitoes (Nematocera). *Pipistrellus kuhlii* only occurs in southern Europe, where it roosts in buildings. They also forage mainly on mosquitoes (Nematocera).

The third group consists of broad-winged and slow-flying species that are highly maneuverable. They prefer to search for food within the cover of vegetation. Also represented in this group are species that eat invertebrates from surfaces (gleaners). Gleaners often eat resting insects in contrast to the previous two groups that forage on flying insects. Another specific foraging technique in this group is to detect prey by listening to the noises they make

instead of using echolocation (flutter-detectors). Flutter-detectors only use echolocation for spatial orientation. This group is represented by several *Myotis spp.*, *Plecotus spp.* and *Rhinolophus hipposideros* (table 1). Several myotis species in this group occur in or near forests (table 1), where there is generally less ALAN present. *Myotis species* eat a variety of invertebrates. Besides the commonly eaten moths (Lepidoptera) and beetles (Coleoptera), they also eat caterpillars (Lepidoptera), ground beetles (Coleoptera), spiders (Araneae), stoneflies (plecoptera), mayflies (Ephemeroptera) and small dragonflies (Odonata). Plecotus species are flutter-detectors that eat moths (Lepidoptera), mosquitoes (Nematocera) and spiders (Araneae). Lastly, *Rhinolophus hipposideros* is a gleaner and flutter-detector that forages on small insects, such as flies (Diptera), mosquitoes (Nematocera), butterflies and moths (Lepidoptera), and spiders (Araneae).

Myotis dasycneme and *Myotis daubentonii* are difficult to group, because they have different foraging techniques. They fly low over open water to forage (Russo et al., 2019). *M. daubentonii* is a relatively slow-flying bat. *M. daubentonii* sleeps in trees and eats mosquitoes (Nematocera), butterflies (Lepidoptera) and beetles (Coleoptera) (Russo et al., 2019). *M. dasycneme* sleeps in buildings and eats mosquitoes (Nematocera), damselflies (Odonata), beetles and butterflies (Lepidoptera) (table 1).

The different diets of bat species are relevant for their response to ALAN, because insects are also heavily influenced by ALAN. The decline in insects that has been persistent over the last decades is a worrying trend, that ALAN is likely contributing to by affecting various aspects of an insects' life (Owens et al., 2020). Many insects are positively phototactic, meaning that they are attracted to light. As a result they swarm around street lights, exhausting or injuring themselves while also being vulnerable to predation (Owens et al., 2020; Eisenbeis, 2006). Some insects are repelled by street lights, likely due to the perceived or actual increased predation risk (Owens et al., 2020). The different responses to light between species can lead to a change in species distribution and species composition in illuminated areas. This can affect the foraging behaviour and/or success of bats. Considering that bats eat different insects, some bat species may be more affected than others. Therefore it is relevant to examine the influence of ALAN on the insect prey.

The research question was answered with multiple studies and review papers. All studies were done in Europe. The majority of studies illuminated a previously dark environment and measured the difference in abundance of bat species. Bat activity was usually measured with a bat detector and sometimes observations were done. In the study of Spoelstra et al. (2017) they illuminated a forest in the Netherlands with differently coloured lights with an intensity comparable to street lights. In the Netherlands they also illuminated culverts that function as a commuting route for bats (Spoelstra et al., 2018). Kuiiper et al. (2008) illuminated commuting routes of *M. dasycneme* in the Netherlands. Zeale et al. (2018) illuminated hedge rows along commonly used commuting routes of *R. hipposideros* in South-West England. Similarly, Stone et al. (2009) illuminated hedges in England. Russo et al. (2017) tested the effect of LED lighting on bats and insects in a riverine ecosystem in Italy. They also sampled insects with sticky traps at different distances from the lights. Rydell et al. (2017) had a different approach and compared the location of bat maternity roosts in churches before and after they were illuminated. Boldogh et al. (2007) illuminated buildings with bat colonies in Hungary. There was one GPS study done by Voigt et al. (2020). They equipped 20 male bats (*Nyctalus noctula*)

with miniaturized GPS loggers in the urban area of Berlin and related spatial positions of bats to anthropogenic and natural landscape features and levels of ALAN. Lastly, the insect studies used either light traps or normal traps to determine the amount of light attraction (Bauer, 1993; Eisenbeis, 2006).

Table 1: The conservation status, occurrence, size, roosting places, diet and foraging technique of several bat species in Europe.

Species	Occurrence	Size	Roosting place	Diet and foraging technique	References
<i>Myotis bechsteinii</i>	Near threatened.	Medium	Trees	Forages on insects in a closed environment	Jones & Rydell., 1994
<i>Myotis Brandtii</i>	Not threatened. Occurs in forest areas.	Small	Trees and buildings	Forages on small insects in a closed environment.	
<i>Myotis dasycneme</i>	Near threatened. Occurs in wet areas.	Large	Buildings	Forages on mosquitoes (nematoceras), caddisflies (trichoptera), beetles (coleoptera) and butterflies (lepidoptera) by flying back and forth in straight lanes ~50 cm above the water.	Kuijper et al., 2008 Jones & Rydell., 1994
<i>Myotis daubentonii</i>	Not threatened.	Medium	Trees	Forages on mosquitoes (nematoceras), butterflies (lepidoptera) and beetles (coleoptera) above water.	Russo et al. 2019 Spoelstra et al., 2017 Jones & Rydell., 1994
<i>Myotis emarginatus</i>	Not threatened.	Medium	Buildings and caves	Forages on spiders (araneae) and flies (diptera) in a closed environment (often in stables)	Boldogh et al., 2014
<i>Myotis myotis</i>	Not threatened.	Large	Buildings and caves	Forages on insects in a closed environment. Gleaner	Jones & Rydell., 1994
<i>Myotis mystacinus</i>	Not threatened.	Small	Trees and buildings	Forages on mosquitoes (nematoceras), flies (diptera), mayflies (ephemeroptera), moths (lepidoptera), beetles (coleoptera) and spiders (araneae) in a closed environment.	Jones & Rydell., 1994

<i>Myotis nattereri</i>	Not threatened. Mainly occurs in forest areas	Medium	Trees	Forages on resting insects, caterpillars (lepidoptera) and spiders (araneae) in a closed environment. Gleaner	Spoelstra et al., 2017 Zeale et al., 2018 Jones & Rydell., 1994
<i>Eptesicus serotinus</i>	Not threatened. Common	Medium	Buildings	Forages on moths (lepidoptera) and beetles (coleoptera) in open/semi-open environment by flying back and forth in straight lines.	Rydell Spoelstra et al., 2017 Jones & Rydell., 1994
<i>Eptesicus nilssonii</i>	Not threatened. Occurs in northern and mountainous areas	Medium			Rowse et al., 2015 Jones & Rydell., 1994
<i>Nyctalus noctula</i>	Not threatened.	Medium	Trees	Forages on moths (lepidoptera), beetles (coleoptera), mosquitoes (nematocera), flies (diptera), caddisflies (trichoptera) and net-winged insects (neuroptera) by flying back and forth in straight lines.	Rydell Spoelstra et al., 2017 Voigt et al., 2020 Jones & Rydell., 1994
<i>Nyctalus leisleri</i>	Not threatened. Occurs in forest areas	Medium	Trees	Forages on mosquitoes (nematoceras), flies (diptera), moths (lepidoptera), beetles (coleoptera) and mayflies (ephemeroptera) by flying back and forth in straight lines.	Jones & Rydell., 1994
<i>Pipistrellus kuhlii</i>	Not threatened. Occurs in Southern Europe	Small			Rowse et al., 2015 Russo et al., 2017
<i>Pipistrellus nathusii</i>	Not threatened. Common	Small	Trees	Forages on mosquitoes (nematoceras) in a semi-open environment.	Zeale et al., 2018
<i>Pipistrellus pipistrellus</i>	Not threatened.	Small	Buildings	Forages on all flying insects in an open/semi-open environment.	Spoelstra et al., 2017 Zeale et al., 2018

					Rowse et al., 2015 Russo et al., 2019 Jones & Rydell., 1994
<i>Pipistrellus pygmaeus</i>	Not threatened.	Small	Buildings	Forages on all flying insects in an open/semi-open environment.	
<i>Plecotus auritus</i>	Not threatened.	Medium	Trees and buildings	Forages silently on moths (lepidoptera), mosquitoes (nematocera) and spiders (araneae) in a closed environment. Gleaner	Spoelstra et al., 2017 Rydell et al., 2017 Jones & Rydell., 1994
<i>Plecotus austriacus</i>	Near threatened.	Medium	Buildings	Forages silently on moths, nematoceras and spiders in a closed environment. Gleaner	
<i>Rhinolophus hipposideros</i>	Not threatened.			Forages on flies (diptera), mosquitoes (nematocera), butterflies and moths (lepidoptera). Flutter-detector	Stone et al., 2009
<i>Vespertilio murinus</i>	Not threatened.	Medium	Trees and buildings	Forages on beetles (coleoptera) and moths (lepidoptera) by flying back and forth in an open environment.	Jones & Rydell., 1994

Effects of ALAN on predation

Flying bats are primarily predated on by aerial hawking birds that hunt by vision, such as owls (Rydell & Speakman, 1995). It has been hypothesized that bats' nocturnality evolved to avoid predation by diurnal avian predators (Rydell & Speakman, 1995). Therefore bats may face or at least perceive, an increased risk of predation when exposed to ALAN. Urban avian predators of bats sometimes extend their activity into nocturnal times as a result of ALAN, and they sometimes exploit the attraction of bats to artificial light sources (Mikula et al., 2016). This is most likely the reason that some bat species avoid light (Spoelstra et al., 2017; Rydell et al., 2017; Rydell, 2006).

Not every species is equally vulnerable to predation, especially slow-flying bats are more vulnerable to predation. This means that *Myotis*, *Plecotus* and *Rhinolophus* species are expected to be more light-deterred (Rydell, 2006). This is shown in multiple studies. The study of Spoelstra et al. (2017) found that *Myotis* and *Plecotus* species significantly decreased activity

at light posts compared to dark conditions (figure 1). This was also found in England for *Myotis* species and *R. hipposideros* (Zeale et al., 2018; Stone et al., 2009). ALAN does not only affect bats when commuting and foraging, but also in choosing a roosting site. One study on the effect of the illumination of maternity roosts in churches showed that *Plecotus auritus* colonies often disappeared after lights were installed outside the church. The colonies that stayed avoided ALAN as much as possible by choosing the darkest path from their roosting site to the vegetation cover (Rydell et al., 2017). Predators often take advantage of the aggregation of bats in roosting places, making a dark roosting place even more important (Mikula et al., 2016). *Myotis Daubentonii* is a slow-flying species that also forages in an open environment. Both these aspects increase the vulnerability of *M. daubentonii* to predation. It was found that the activity of *M. Daubentonii* significantly declined when riverbanks were illuminated (Russo et al., 2017). However, one study found that *M. daubentonii* passing through culverts underneath a road showed no reaction to lighting, regardless of its colour (Spoelstra et al., 2018). A possible explanation of this result is that avian predators cannot hunt bats in culverts. This suggests that the response to light is dependent on circumstances. Similarly, ALAN reduced the foraging activity of *Myotis dasycneme* over rivers in the Netherlands (Kuijper et al. 2008).

The fast-flying *Eptesicus* and *Nyctalus* species were less light-deterred, although they avoided light on occasions as well. In the study of Spoelstra et al. (2017) no difference was found in the abundance of *Nyctalus* and *Eptesicus* species between light and dark conditions. However, a GPS study in Berlin showed that *Nyctalus noctula* avoided light when commuting (Voigt et al., 2020). The group of small fast-flying species (*Pipistrellus* species) did not show light avoidance (Spoelstra et al., 2017; Russo et al., 2019; Zeale et al., 2018; Rydell, 2006).

The light-deterred behaviour of slow-flying species is expected to affect the species negatively. Many illuminated resources become unavailable to them and it can result in habitat fragmentation. For example, illuminated foraging spots and roosting places are not used anymore (Rydell et al., 2017; Russo et al., 2017). This can result in a decrease in fitness for light-deterred bat species. On the other hand, light-opportunistic species may face negative consequences from increased predation.

Effects of ALAN on foraging

The accumulation of flying insects at street lights is interesting to some foraging bats. Positive phototaxis was especially seen in moths, beetles and flies around street lights in Germany (Eisenbeis, 2006). Near bodies of water, the aquatic caddisflies were also found in high proportions. A study by Bauer (1993) compared the number of insects approaching streetlights with the number caught in traps to determine the degree of phototaxis in the insect species. The ratios were especially high for moths, mosquitoes, mayflies and caddisflies. These insect species are commonly eaten by most bat species. Additionally, diurnal and crepuscular insects continue their foraging activities during the night under the influence of ALAN, increasing the amount of insects at street lights even more (Owens et al., 2020).

To the benefit of the foraging bats, defence mechanisms of insects are often impaired near ALAN. The lights can have a strong dazzling effect on insects (Eisenbeis, 2006). As a result, they often become immobilized while flying towards and around the lamp. They end up

resting on the ground or vegetation as a result (Eisenbeis, 2006). This also impairs evasive flight behaviour. An additional problem affecting their evasive flight behaviour is that protective vegetation is often far away from the street lights (Owens et al., 2020). Consequently, insects near ALAN make easy prey for foraging bats. Moths are frequent prey of bats, especially around street lights (Frank, 2006). Most nocturnal moth species have tympanic organs that can hear echolocation calls from bats. When they hear echolocation calls, they show evasive behaviour. However, moths flying around lights do not perform evasive behaviour. Possibly, because they perceive the artificial light as daylight and echolocation calls coming from bats during the day is unlikely (Rydell, 2006). They keep flying around the lamp, making them easy prey for bats (Frank, 2006). Rydell (1992) concluded that bats foraging around street lights typically had a higher food intake. The cause was mainly the consumption of moths, which are larger than the insects they eat in normal habitats. The caloric intake of *Eptesicus nilssonii* was twice as high while hunting moths around streetlamps than while foraging flies in woodlands (Rydell, 1992). A high amount of insects has been shown to attract more bats than a lower amount of insects (Rowse et al., 2015). For example, in the urban city center the density of insects per street light is lower, thus bats are less inclined to forage there. Also, the amount of vegetation cover and the type of light can influence the amount of insects present (Rydell et al., 2017).

It differs per bat species group whether the accumulation of insect species at ALAN is exploited. The medium-sized fast-flying *Nyctalus* and *Eptesicus* species often fly above large illuminated areas, for example car parks and roads, in straight lines (Rydell, 2006). They dive towards insects flying around street lights (Rydell, 2006). *Nyctalus noctula* was more abundant at foraging sites next to bodies of water when they were illuminated (Voigt et al., 2020). Zeale et al. (2018) also found an increase in activity of *Eptesicus* and *Nyctalus* species at ALAN. However, Spoelstra et al. (2017) found no significant change in abundance of *Nyctalus* and *Eptesicus* species near ALAN (figure 1). A possible explanation is that the illuminated areas in this study were relatively small compared to the illuminated areas *Eptesicus* and *Nyctalus* species normally exploit for foraging.

The small fast-flying *Pipistrellus* species especially exploit the accumulation of insects near street lights. They are maneuverable enough to forage around single lamp posts. In multiple studies it has been found that the activity of *Pipistrellus* species increases near lights (figure 1) (Spoelstra et al., 2017; Zeale et al., 2018; Russo et al., 2019). In the study of Spoelstra et al. (2017) they also found a highly significant effect of light on insect abundance and a correlation between insect abundance and the presence of *Pipistrellus* species, suggesting that insect abundance is indeed the cause of the increase in bats near street lights.

In contrast, the slow-flying *Myotis* and *Plecotus* species decrease their activity at lights (Spoelstra et al., 2017; Zeale et al., 2018; Stone et al., 2009). Although *Myotis* and *Plecotus* species sometimes forage on moths, flies, mosquitoes or beetles, they do not take advantage of their accumulation near street lights. The most plausible explanation is that the predation risk is too high for these slow-flying. Additionally, *Myotis* and *Plecotus* species also forage on resting insects, caterpillars, ground beetles and spiders, which do not accumulate at street lights. This makes foraging around street lights less beneficial for them than for the light-opportunistic species mentioned before. Lastly, *M. daubentonii* and *M. dasycneme* were found to reduce foraging activity at illuminated bodies of water (Russo et al., 2019; Kuijper et al. 2008). Even though the insects encountered near ALAN comprised >95% of the diet of *M. daubentonii*

(Russo et al., 2019). Also for these species, the increased predation risk species is likely the cause.

Light-deterred species can experience a disadvantage from the positive phototaxis of invertebrates, besides not exploiting the possible advantage. An illuminated area attracts insects from their habitat from a distance, depleting the darker areas of these insects (Eisenbeis, 2006). For example, in the study of Russo et al. (2019) they trapped six insect groups under lit conditions that were not found under dark conditions at the same location (Hymenoptera, Neuroptera and four Brachyceran families). Many positively phototactic insects fly directly onto the hot surface of the lamp and die immediately (Eisenbeis, 2006). Another possibility is that the insect circles the lamp until it is claimed by injury, exhaustion or predation (Eisenbeis, 2006; Owens et al., 2020). The increased death rate among insects as a result of ALAN impoverishes the natural environment. For example, a 30 year survey of Dutch macromoths showed that nocturnal species underwent steeper declines than diurnal species (van Langevelde et al., 2018). The decrease in prey availability caused by the attraction to light and the increased death rate, is called the vacuum cleaner effect.

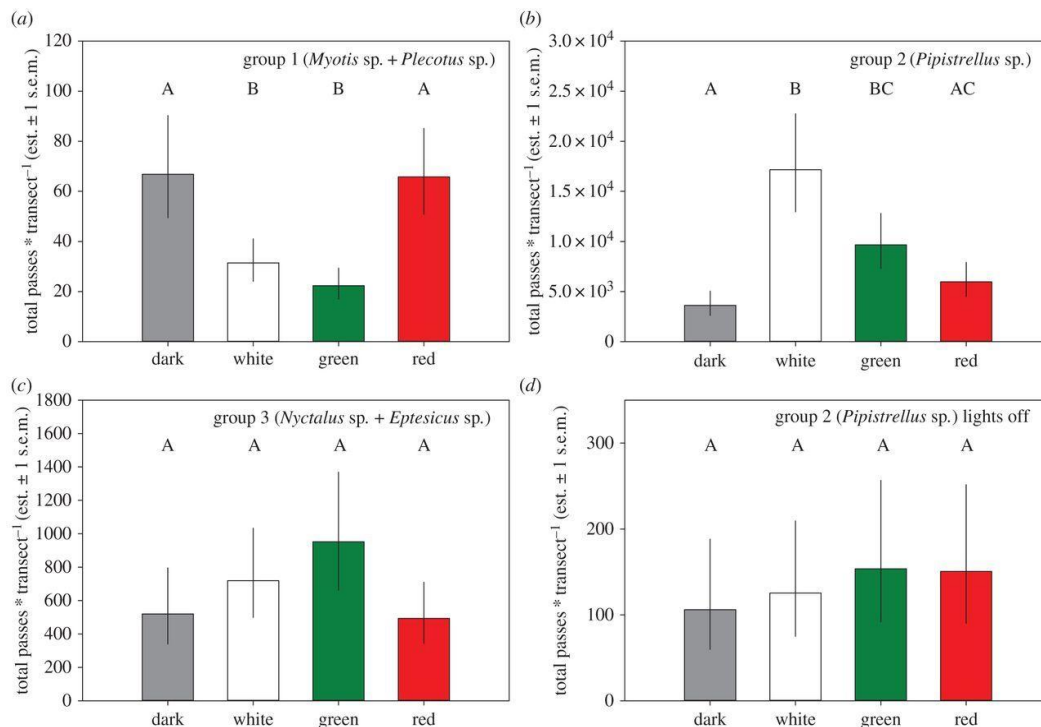


Figure 1. Total bat passes during a study in a forest in the Netherlands per light treatment (either dark, white light, green light or red light) during all years 2012-2016 for (a) group 1 (*Myotis* and *Plecotus* species), (b) group 2 (*Pipistrelli* species), (c) group 3 (*Nyctalus* and *Eptesicus* species) and (d) passes of group 2 bats during nights when the lights were off for moth sampling. Capitals identify groups that significantly differ from each other in post hoc tests. Note. From “Response of bats to light with different spectra : light-shy and agile bat presence is affected by white and green, but not red light,” by Spoelstra, K., Grunsvan, R. H. A. Van, Ramakers, J. J. C., Kim, B., Raap, T., Donners, M., Veenendaal, E. M., Visser, M. E., & Visser, M. E. (2017), *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329(8–9), 506–510.

Bats emerge in the evening from their roosting places. The emergence time roughly follows the time of sunset (DeCoursey & DeCoursey, 1964). The amount of time in between sunset and emergence differs per species, based on their diet and flight speed. The reason for that is that the evolution of the optimal emergence time was under the influence of food availability and predation risk (Jones & Rydell, 1994). Around dusk, there is a peak in flying insect activity of mosquitoes and other small flies, which gives an advantage to emerge earlier for species foraging on small flying insects. However early emergence leads to an increased risk of predation by diurnal birds that are still active. Thus among species that have a similar diet, faster flying species tend to emerge earlier.

In figure 2 (Jones & Rydell, 1994) the emergence time is set out against different diets. The species with the earliest emergence time are *Nyctalus* and *Eptesicus* species (Jones & Rydell, 1994). They are fast flyers that forage on mosquitoes and other small flying insects. Afterwards, slower species that also forage on small flying insects and on moths emerge. In this group are the *Pipistrellus pipistrellus*, *Vespertilio murinus*, *Myotis mystacinus*, *myotis bechsteinii* and *Rhinolophus hipposideros* (Jones & Rydell, 1994). Species that forage mainly on moths do not experience an advantage when emerging earlier, while moths are active throughout the night. The gleaners, such as *Myotis myotis* and the *Plecotus* species, emerge even later. This foraging technique requires slow flight, which makes them more vulnerable to predation. This is one of the reasons that they emerge later. Additionally, they do not benefit from the increase in insect flight activity around dusk, because they glean insects from surfaces. Lastly, *M. daubentonii* and *M. dasycneme* emerge. They forage slowly and low over open water, making them most vulnerable to predation (Russo et al., 2019; Jones & Rydell, 1994).

Bats determine the right time to emerge by the amount of light outside their roosting places (DeCoursey & DeCoursey, 1964). Several studies found that an increase or decrease in light by artificial lamps or weather conditions would respectively lead to a later or earlier emergence time (DeCoursey & DeCoursey, 1964). Consequently, bats roosting in illuminated places have a later emergence time (Boldogh et al., 2014). For all bats this results in a shorter foraging period, but the severity of the consequences can differ per species. The species that exploit the peak of flying insects around dusk are especially sensitive to good timing. When they emerge too late, they can miss the peak in insect activity. As a result, they can have a decreased food intake (Boldogh et al., 2014). However, insects have been shown to continue their activity in the night under the influence of ALAN (Owens et al., 2020). Thus, it is expected that the problem mainly occurs when the amount of ALAN at the roosting place does not match the amount of ALAN at the foraging location. This is likely to occur when buildings get illuminated.

Myotis species and *Plecotus* species that often wait until it is dark before they emerge face a different problem. Due to ALAN it might never get completely dark, shortening the activity period of these species severely. Sometimes colonies do not emerge at all when their roosting place is brightly illuminated (Boldogh et al., 2014). In the study of Boldogh et al. (2014) they also found that juveniles of the house-dwelling *Myotis emarginatus* had a lower body mass in illuminated roosting places than juveniles in dark roosting places. *Myotis* and *Plecotus* species

sometimes leave their illuminated roosting places completely (Boldogh et al., 2014; Rydell et al. 2017).

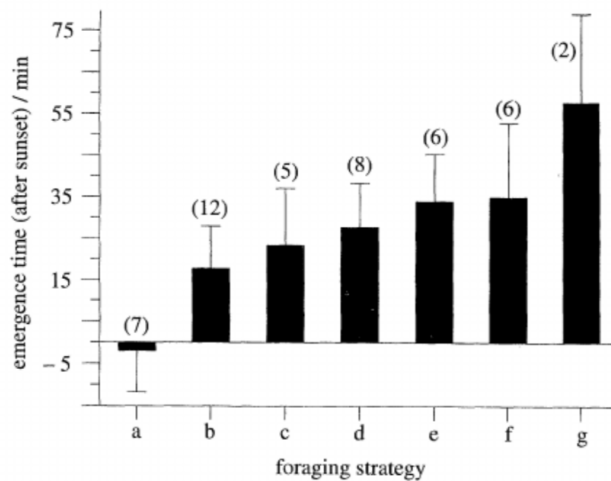


Figure 2. Time of emergence in relation to diet for bats grouped into seven foraging classes: a, tropical species that feed mainly on small aerial insects; b, their temperate zone counterparts; c, tropical species that feed mainly on moths; d, their temperate zone counterparts; e, temperate zone bats that feed mainly on flightless or diurnal arthropods, i.e. gleaners; f, tropical bats that feed mainly on fruit, nectar or pollen; and g, temperate zone bats that mainly feed low over water. Columns show mean positive standard deviations for each class, with sample sizes (number of species) in brackets above.

Note. From “Foraging strategy and predation risk as factors influencing emergence time in echolocating bats,” by Jones, G., & Rydell, J., 1994, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 346(1318), 445–455. <https://doi.org/10.1098/rstb.1994.0161>.

Discussion

The behaviour of bats around ALAN is largely determined by their flight speed and foraging technique. The negative effects of ALAN on predation risk and the positive effects of ALAN on prey availability result in a trade-off with different outcomes for different species. Both the medium-sized fast-flying species (*Eptesicus* and *Nyctalus* spp) as the small fast-flying species (*Pipistrellus* spp) are light-opportunistic. Their fast flight enables them to exploit ALAN for foraging, even though there is an increased predation risk. When commuting, however, ALAN does not provide an advantage to bats. That could be the reason that *Nyctalus* spp avoided ALAN during commute (Voigt et al., 2020). Consequently, they can still experience some amount of habitat fragmentation. The same trade-off between prey availability and predation risk is made for their emergence time. They emerge early to exploit the increase in insect flight activity around dusk, but not too early in order to avoid diurnal predators (Jones & Rydell, 1994). Illuminated roosting places can result in a mismatch in timing with the peak in prey availability and predator activity. Possibly, light-opportunistic species also live in more urban environments. Therefore they would face the problem of an illuminated roosting place more often than light-deterred species. This gives them a disadvantage, because they have a

shorter foraging time. The severity of these advantages and disadvantages is hard to determine. Light-opportunistic species are likely to increase as a result of the increased food intake. However, increased predation and the disadvantage of roosting in an illuminated environment could counteract the advantage of increased food intake. Whether that is the case is difficult to say. The degree of increased predation risk that bats experience is uncertain and likely to differ per location. Also, it is difficult to obtain reliable population estimates of bats (Rydell, 2006). Therefore it is not certain whether there have been changes in the amount of light-opportunistic bats.

The slow-flying maneuverable species (*Myotis* and *Plecotus* species) and the species foraging above water (*Myotis daubentonii* and *M. dasycneme*) are light-deterred. As a result they experience decreased prey availability, habitat fragmentation, less available roosting places, less available foraging places and a shorter foraging period in illuminated environments. The light avoiding behaviour is also reflected in their late emergence time. When sleeping in illuminated buildings, this can cause a decrease in food intake (Boldogh et al., 2014). Their light avoiding behaviour saves them from predators, but the many disadvantages are likely to lead to a decline in bats from these species. This is especially concerning since some *Myotis* and *Plecotus* species are already near threatened (table 1).

The behaviour of the different bat species was mostly consistent across multiple studies and multiple countries, suggesting that their behaviour is static. Rydell (2006) found that only a few rare species, such as the *Barbastella barbastellus*, were shown to alter their behaviour around lights. This also means that it is less likely that negatively affected bat species will adapt to their illuminated environment.

Based on this review, it would be expected that light-deterred species decrease relative to light-opportunistic species. Light-deterred species experience only disadvantages, while light-opportunistic species experience one large advantage. However, whether ALAN causes a decrease or increase in population size is also under the influence of many factors that are not taken into account here. For example, many bats migrate and ALAN affects their navigation. ALAN could also affect their circannual timing. Additionally, the interactions between different species are not addressed in this paper. Imagineably, competition over similar resources plays a large role in species composition and distribution. An increase in light-opportunistic species could influence the amount of available prey and roosting places for light-deterred species. Similarly, the predator-prey relation between bats and insects is severely impacted by ALAN due to the influence of ALAN on both predators and prey. This review provides the information on species level to be able to address consequences of ALAN on the predator-prey relationship and bat species composition in the future.

References

Bauer, R. 1993. Untersuchung zur Anlockung von nachtaktiven Insekten durch Beleuchtungseinrichtungen [Investigation of the attraction of nocturnal insects by artificial lights]. Diploma thesis, Department of Biology, University of Konstanz, Germany

Boldogh, S., Dobrosi, D. & Samu, P. (2007). The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica*. 9(2). 1508-1109. [https://doi.org/10.3161/1733-5329\(2007\)9](https://doi.org/10.3161/1733-5329(2007)9)

DeCoursey, G., & DeCoursey, P.J. (1964). Adaptive Aspects of Activity Rhythms in Bats. *The Biological Bulletin*, 126(1), 14–27. <https://doi.org/10.2307/1539413>

Eisenbeis, G. (2006). Artificial Night Lighting and Insects: Attraction of Insects to Streetlamps in a Rural Setting in Germany. In Rich, C. & Longcore, T. *Ecological Consequences of Artificial Night Lighting* (pp. 281-304). Island Press.

Frank, D.K. (2006). Effects of Artificial Night Lighting on Moths. In Rich, C. & Longcore, T. *Ecological Consequences of Artificial Night Lighting* (pp. 305-344). Island Press.

Jones, G., & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 346(1318), 445–455. <https://doi.org/10.1098/rstb.1994.0161>

Kuijper, D.P.J., Schut, J., Dulleman, D., Limpens, Toorman, H., goossens, N. & Ouwehand, Janne. (2008). Experimental evidence of light disturbance along commuting routes of Pond bats *Myotis dasycneme*. *Lutra*, 51, 37-49.

Mikula, P., Morelli, F., Lučan, R. K., Jones, D. N., & Tryjanowski, P. (2016). Bats as prey of diurnal birds: SA global perspective. *Mammal Review*, 46(3), 160–174. <https://doi.org/10.1111/mam.12060>

Owens, A. C. S., Cochard, P., Durrant, J., Farnworth, B., Perkin, E. K., & Seymoure, B. (2020). Light pollution is a driver of insect declines. *Biological Conservation*, 241, 0006-3207. <https://doi.org/10.1016/j.biocon.2019.108259>

Rich, C. & Longcore, T. (2006). *Ecological Consequences of Artificial Night Lighting*. Island Press.

Rowse, E.G., Lewanzik, D., Stone, E.L., Harris, S. & Jones, G. (2015). Dark Matters: The Effects of Artificial Lighting on Bats. In Voigt, C. C., & Kingston, T. *Bats in the anthropocene: Conservation of bats in a changing world* (pp. 187-213). Springer International.

Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P., & Ancillotto, L. (2019). Artificial illumination near rivers may alter bat-insect trophic interactions. *Environmental Pollution*, 252, 1671–1677. <https://doi.org/10.1016/j.envpol.2019.06.105>

Rydell, J. (1992). Exploitation of Insects around Streetlamps by Bats in Sweden. *Functional Ecology*, 6(6), 744-750. doi:10.2307/2389972

Rydell, J., & Speakman, J. R. (1995). Evolution of nocturnality in bats: Potential competitors and predators during their early history. *Biological Journal of the Linnean Society*, 54(2), 183–191. <https://doi.org/10.1006/bijl.1995.0011>

Rydell, J. (2006). Bats and their insect prey. Ecological Consequences of Artificial Night Lighting. In Rich, C. & Longcore, T. *Ecological Consequences of Artificial Night Lighting* (pp. 43-60). Island Press.

Rydell, J., Eklöf, J., & Sánchez-Navarro, S. (2017) Age of enlightenment: long-term effects of outdoor aesthetic lights on bats in churches. *Royal Society Open Science*, 4(12), 1–8. <http://doi.org/10.1098/rsos.161077>

Spoelstra, K., Grunsvan, R. H. A. Van, Ramakers, J. J. C., Kim, B., Raap, T., Donners, M., Veenendaal, E. M., Visser, M. E., & Visser, M. E. (2017). Response of bats to light with different spectra : light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the royal society B-biological sciences*. 284(1855), 0962-8452. 10.1098/rspb.2017.0075

Spoelstra, K., Ramakers, J. J. C., van Dis, N. E., & Visser, M. E. (2018). No effect of artificial light of different colors on commuting Daubenton's bats (*Myotis daubentonii*) in a choice experiment. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329(8–9), 506–510. <https://doi.org/10.1002/jez.2178>

Stone, E. L., Jones, G., & Harris, S. (2009). Street Lighting Disturbs Commuting Bats. *Current Biology*, 19(13), 1123–1127. <https://doi.org/10.1016/j.cub.2009.05.058>

van Langevelde, F, Braamburg-Annegarn, M, Huigens, ME, et al. Declines in moth populations stress the need for conserving dark nights. *Glob Change Biol*. 2018; 24: 925– 932. <https://doi-org.proxy-ub.rug.nl/10.1111/gcb.14008>

Voigt, C. C., Scholl, J. M., Bauer, J., Teige, T., Yovel, Y., Kramer-Schadt, S., & Gras, P. (2020). Movement responses of common noctule bats to the illuminated urban landscape. *Landscape Ecology*, 35(1), 189–201. <https://doi.org/10.1007/s10980-019-00942-4>

Zeale, M. R. K., Stone, E. L., Zeale, E., Browne, W. J., Harris, S., & Jones, G. (2018). Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats. *Global Change Biology*, 24(12), 5909–5918. <https://doi.org/10.1111/gcb.14462>

