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Light or flight?

The impact of artificial light at night on insect predation risk

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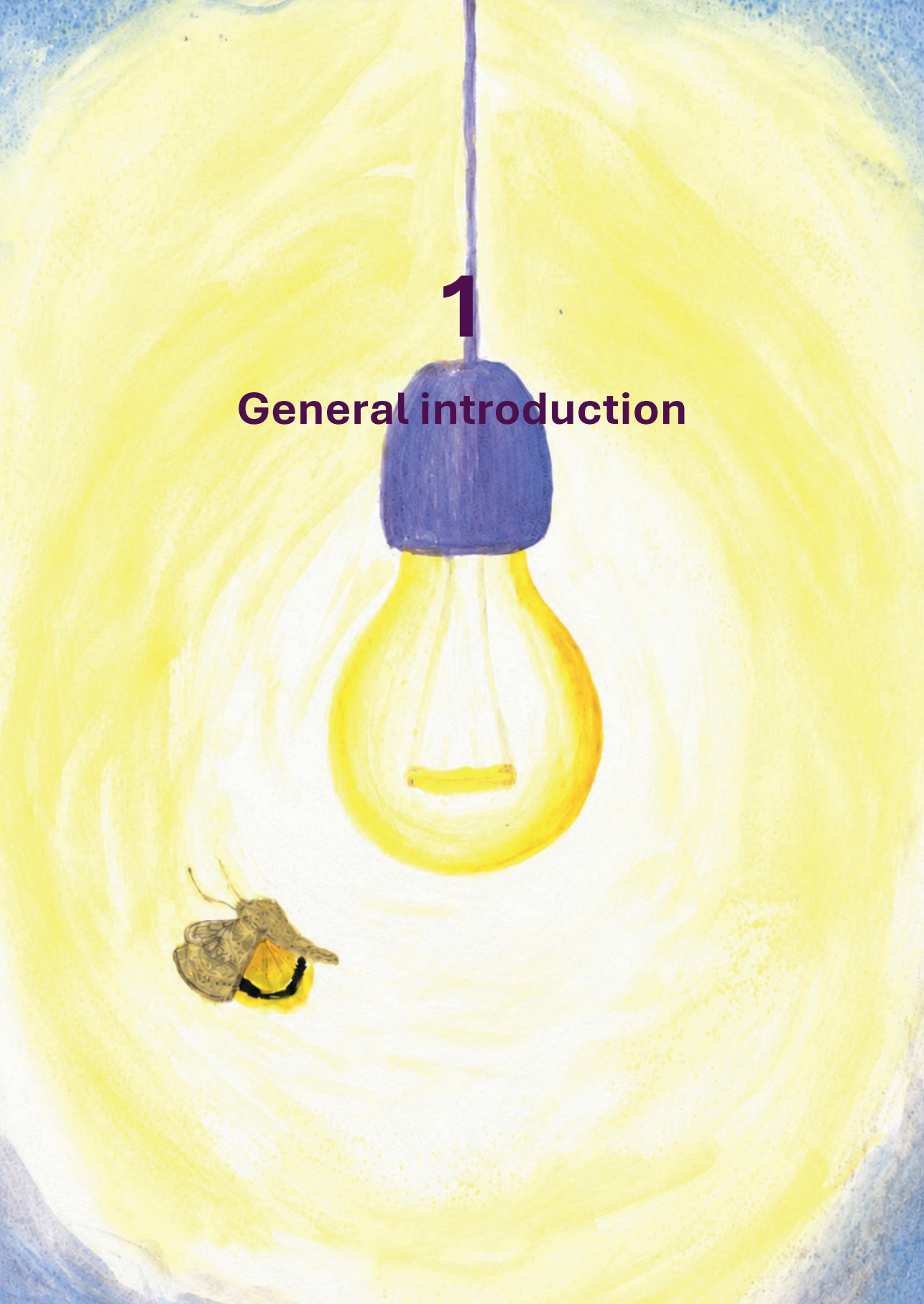
General introduction



This thesis examines the impact of artificial light at night (ALAN) on predator-prey interactions. In this chapter, I begin by introducing the general problem of ALAN, with a particular focus on the ecological consequences of light pollution. I then concentrate on how ALAN alters predator–prey dynamics, outlining the different pathways through which ALAN disrupts these interactions. Finally, I present the structure of this thesis and briefly introduce the objectives and main themes of the subsequent chapters.

1. Artificial light at night (ALAN)

1.1. Description

Artificial light at night, also called anthropogenic light at night (ALAN) (Durmus, 2024), encompasses all the light that has been added to the night sky by human influence. The first human-created light came in the form of fire. Later it developed to gaslight, which slowly spread the human usage of light. Finally, with the invention of electrical light the true proliferation began, fundamentally transforming the nightscape (Kyba et al., 2011).

ALAN consists of direct light from discrete light sources (e.g. streetlights, building lights) and skyglow (Grenis et al., 2023; Van de Schoot et al., 2025). Skyglow is the indirect light that brightens the sky, caused by light scattering through the air and reflecting off atmospheric particles (Kyba et al., 2011). Through the process of air scattering, light can move several kilometers away from its origin, affecting areas without any primary light sources (Jechow et al., 2020; Kyba et al., 2015).

Characteristically, ALAN is very different from natural light. It appears at very unusual times and places (Falchi et al., 2016) and can reach intensities and spectra unprecedented by natural light sources (Dominoni & Nelson, 2018). For example, typical moonlight illumination is estimated to be around 0.05–0.30 lux at ground level, depending on the moon phase (Kyba et al., 2017), whereas a regular streetlight can be up to 800 times brighter, ranging from 10 to 40 lux at ground level (Gaston et al., 2017).

1.2. Dynamics and global extent

Currently, sky brightness increases globally at an annual average rate of 2.2%-9.6% (Hölker et al., 2010; Kyba et al., 2017, 2023). ALAN is closely tied to urban development (Jechow et al., 2020; Walker, 1977). As the human population grows, driving the expansion of human infrastructure and the spread of urban areas, ALAN expands accordingly (Gu et al., 2021). However, the rate at which ALAN emissions increase even surpasses the rate of population growth (Gaston & Miguel, 2022), intensified by the continuous development of more efficient lighting technologies, such as Light Emitting Diodes (LED) (Sánchez de Miguel et al., 2021).

Presently, more than 80% of the human population lives in light polluted areas (Falchi et al., 2016). These bright night skies prevent one-third of the human population from seeing the Milky Way from where they live (Falchi et al., 2016).

1.3. Associated costs

ALAN has enabled people to extend their productivity and social life into the night time niche, and has ameliorated our sense of safety (Himschoot et al., 2024; but not necessarily the actual safety (Gaston et al., 2015)). However, ALAN also comes with a price.

First, there is an enormous economic cost to ALAN. Expenses are estimated to account for 0.72% of the global gross domestic product, as seen in 2010 (Tsao et al., 2010). When factoring in the costs associated with the loss of ecosystem services due to ALAN, this adds an additional 2.87 trillion euros per year (Anderson et al., 2024).

Electric lighting consumes about 17-20% of the globally produced electricity (Zissis, 2016), with public lighting accounting for approximately 2.3% (Lobão et al., 2015; Zissis, 2016). This way, electrical lights contributes a substantial 6% to our carbon dioxide emissions, promoting climate change (United Nations Environment Programme, 2013).

On top of the economic cost and the carbon footprint, light also acts as a sensory pollutant. Generally, we distinguish between two types of light pollution: astronomical light pollution and ecological pollution (Longcore & Rich, 2004). Astronomical light pollution entails the concealment of the night sky and celestial bodies (Longcore & Rich, 2004), which hampers astronomy but is also seen as a cultural loss for humankind (Varela Perez, 2023). Ecological light pollution describes the obscuration of the natural light-dark cycle and celestial cues, which is associated with a variety of ecological disturbances (Longcore & Rich, 2004).

1.4. Ecological light pollution

The spinning movement of planet Earth creates a rhythmic pattern of light and darkness. This roughly 24-hour cycle also shows seasonal variation. On top of that, the moon adds its own illuminance cycle, transitioning from the low-light conditions of the new moon to the high brightness of the full moon. Life that emerged on Earth evolved under these natural light-dark patterns, making light a central part in the functioning of organisms. Light became a key resource in vital processes, such as photosynthesis. However, darkness is equally essential, for example, to recover from oxidative stress or ozone damage (Queval et al., 2007; Vollsnes et al., 2009). Furthermore, the light-dark cycle sustains the circadian and circannual rhythms of species, timing a myriad of

internal and behavioural processes (Johnsson, 2008). The temporal niches provided by these dark and light periods allow for niche partitioning between species, helping to avoid competition and predation (Gutman & Dayan, 2005; Jones & Rydell, 1994). Light also has an important role in the spatial orientation of species (Deutschlander et al., 1999; Fabian et al., 2024; Smolka et al., 2016). Finally, light is an essential component in visual perception (Briolat et al., 2021).

When ALAN emerged, the natural light-dark cycle blurred and new light sources appeared, affecting the temporal, spatial and spectral signature of light (Gaston et al., 2013). Since natural light is at the basis of biological organisation, ecological light pollution has disrupted a myriad of processes. Many genetic, physiological and behavioural consequences have been found on an individual level (e.g. Khan et al. 2018; Elgert et al., 2020; Altermatt and Ebert, 2016), which in turn can influence the distribution and abundances of populations (e.g. Duarte et al., 2019; Van Langevelde et al., 2017) and alter community compositions and food web interactions (e.g. Knop et al., 2017; Davies et al., 2015; McMunn et al., 2019).

Evidence from both terrestrial and aquatic systems shows that ALAN affects a broad diversity of organisms, from microorganisms (e.g. Ayalon et al., 2021; Bari, 2024; Li et al., 2024; Maggi et al., 2020) to plants (e.g. Cieraad et al., 2023; Meng et al., 2022), fungi (e.g. Wang et al., 2024) and animals, invertebrates (e.g. Cai et al., 2025; Gao et al., 2024; Gomes, 2020; Jahnsen-Guzmán et al., 2025; Willmott et al., 2019) and vertebrates (e.g. Dominoni et al., 2020; Forsburg et al., 2021; Hermans et al., 2024; Pulgar et al., 2019; Thawley & Kolbe, 2020). However, the most negative consequences of ALAN are most likely to be found in nocturnal species, as their traits have been tailored to darkness (Ditmer et al., 2021; van Langevelde et al., 2018). This is substantial, as 30% of vertebrates and more than 60% of invertebrates are nocturnal (Hölker et al., 2010).

1.5. Impact on predator-prey interactions

This thesis focusses on the impact of ALAN on predator-prey interactions. Predation is an ecological interaction in which one organism kills and consumes all or a substantial fraction of another organism (Abrams, 2000). Through this interaction, predators and prey strongly influence each other's fitness, as predator-prey dynamics shape individual survival, recruitment, behaviour, habitat choice, foraging, growth, energy allocation, and ultimately species distributions and community interactions (Beauchamp, 2007). Given its direct effects on fitness, the behaviours and morphological traits that determine the outcomes of predator-prey interactions are often subject to strong natural selection (Abrams, 2000).

Because predator-prey interactions are key components of food webs, a good understanding of the effects of ALAN on predator and prey activities and behaviours is important to understand community-level consequences of light pollution. Previous research has shown that ALAN can cause varying outcomes in predator-prey interactions depending on the system at hand. While several studies reported an increase in predation (Mcmunn et al., 2019; Miller et al., 2017; Nuñez et al., 2021), others reported decreased predation under ALAN conditions (Eckhartt & Ruxton, 2022; Jackson et al., 2025). In addition, there were cases where ALAN did not impact the amount of predation (Amoroso, 2024; Grenis et al., 2015). Thus, outcomes of ALAN on these species interactions are context and species specific (Seymoure et al., 2023).

The main mechanisms by which ALAN can directly cause shifts in predator-prey interactions are through its impact on spatio-temporal niche overlap, alterations in visual ecology and behavioural interference.

1.5.1. Shifts in spatial niche overlap

ALAN acts as a spatial organiser. While certain species move towards light (Charvalakis et al., 2025; Eccard et al., 2018; Rebke et al., 2019; Spoelstra et al., 2017; Willmott et al., 2019), others move away from it (Berger et al., 2020; Eccard et al., 2018; Sanna et al., 2024; Spoelstra et al., 2017; Vowles & Kemp, 2021). Thereby, ALAN can greatly influence the spatial niche overlap between species, which is essential for them to interact. Several mechanisms can be at play.

Firstly, ALAN can disorient animals. Many species use light for their spatial orientation, so ALAN can act as a false spatial cue, misguiding species and causing them to inadvertently end up in the light sphere. This mechanism likely at least partly explains the capturing effect of artificial lights, evident in both nocturnally migrating birds and insects congregating around light sources (Charvalakis et al., 2025; Rebke et al., 2019). Insects from different orders tilt their dorsum towards the light (Fabian et al.,2024). Under normal conditions, i.e. under a naturally lit sky, this behaviour helps insects to stay upright. However, near artificial light sources this behaviour leads to continuously steering around the light. For birds, ALAN has the potential to interfere with all their main orientation strategies, including solar, stellar, and magnetic orientation (Adams et al., 2021).

Secondly, light can be associated with positive or negative fitness outcomes, thereby actively attracting or deterring species. For many, often nocturnal species, light is likely associated with an increased predation risk (Prugh & Golden, 2014). Therefore, these prey species prefer darkness and are deterred by ALAN (Spoelstra et al., 2017). Their ALAN-triggered alertness may also make them hide more and avoid open areas

(Dissegna & Chiandetti, 2025; Rotics et al., 2011), adding another layer to this spatial filtering beyond phototaxis.

On the other hand, ALAN can be attractive because of the associated foraging gains. Certain taxa can benefit from the local increases in light-attracted insects around a light source (González-Bernal et al., 2016; Heiling, 1999; Hermans et al., 2024). Others can benefit from the increased search efficiency in a lit foraging patch (Santos et al., 2010).

There are likely many more positive or negative phototactic behaviours that may be affected by ALAN, such as light-associated mating, temperature or moisture regulation, etc. (Kadochová et al., 2019; Seiger & Woodruff, 1987; Togashi et al., 1999). However, throughout this thesis I focus only on the mechanisms described above, as these are the most likely to explain our observations.

1.5.2. Shifts in temporal overlap

Light partitions the day into several temporal niches, creating distinct activity periods: diurnal (day-active), nocturnal (night-active), crepuscular (active during twilight), and cathemeral (active at irregular intervals during both day and night) (Seymoure et al., 2023). Many species have evolved distinct activity patterns that minimise predation risk by exploiting temporal niches in which their predators are less active or less efficient (Cunningham et al., 2019; Helm et al., 2017). Since ALAN affects circadian rhythms (Dominoni et al., 2022; Duarte et al., 2019), shifts in predator-prey interactions are likely to occur.

ALAN has created the so-called night light niche (Longcore & Rich, 2004; Schwartz & Henderson, 1991). For example, predators which are usually limited to daytime activity can extend their foraging into the nighttime with ALAN. Evidence for this night light niche comes from a taxonomically diverse range of predators (Dwyer et al., 2013; Frank, 2009; Lebbin et al., 2007; Maurer et al., 2019; Miller et al., 2017). Diurnal species that exploit the night light niche might also become prey for nocturnal predators that are not deterred by the light (Henke et al., 2022). Conversely, the activity of nocturnal species might be delayed or inhibited, reducing predator-prey encounters (Matsushige & Hibino, 2023; Moyse et al., 2023; Stone et al., 2009).

1.5.3. Impact on visual ecology

ALAN can alter the visual capacity of species and play an important role in the visual ecology of predator and prey, thereby affecting foraging efficiency and prey selection (Briolat et al., 2021; Cole et al., 2019). This is especially true for diurnal species that mainly rely on their well-developed photopic vision. For them, ALAN can be a useful

tool allowing them to extend their activity into the night (Cerveira et al., 2019). However, the prey detection of some nocturnal species may also increase when they use vision as one of their sensing modalities (Amoroso, 2024; Passarotto et al., 2025).

As well as influencing visual acuity, ALAN can affect colour discrimination in predators. Broad-spectrum light in particular can have a profound impact on colour perception (McMahon et al., 2022). As such, ALAN can affect the effectiveness of camouflage (McMahon et al., 2022; Moyse et al., 2023). For example, the relative predation rate by intertidal crabs on two cryptic colour morphs of aquatic snails switched under ALAN compared to control nights (Moyse et al., 2023). Although less studied in the context of ALAN, the effectiveness of aposematic and deflective colour patterns depends on natural light conditions (Nokelainen et al., 2022; Olofsson et al., 2010; Rojas et al., 2014), suggesting that these strategies are also likely impacted by ALAN. Furthermore, alternative colour-based foraging preferences developed under different artificial light environments can become fixed in populations after several generations of exposure (Cole et al., 2019), indicating that ALAN can exert strong selection pressures.

ALAN can also affect selection on colours in prey, which can be especially important for those that use camouflage. To be less conspicuous, cryptic prey benefit from a matching background, either by a proper background choice or by adapting their own colours to the background. However, ALAN can impede this process, making the prey more conspicuous in their environment. For example, the marine isopod *Ligia Oceanica* (Ligiidae) sought out darker backgrounds more often under diffuse ALAN conditions, while they themselves turned lighter (Bullough et al., 2023).

1.5.4. Behavioural interference

Finally, ALAN can interfere with the behaviours of both predator and prey, altering their performance (Minnaar et al., 2015). A well-known example of such behavioural interference is the impairment of evasive flight manoeuvres in eared moths under ALAN conditions (Minnaar et al., 2015; Wakefield et al., 2015). Under normal conditions, tympanate moths initiate last-ditch evasive manoeuvres after detecting the echolocation calls of hunting bats, but under ALAN conditions they often fail to do so. A possible explanation for this interference could be that this defensive reaction is not adaptive during daytime when bats are not active and that this behaviour is therefore limited under ALAN conditions (Svensson et al., 2003). Other forms of behavioural interference are also possible. For example, nocturnal wolf spiders start moving later under ALAN, which can impede their foraging ability (Amoroso, 2024). A similar freezing effect has been found in isopod prey under ALAN, where a postponed escape could increase its vulnerability to predation (Dissegna & Chiandetti, 2025). All these behavioural alterations can greatly impact the efficiency of both predator and prey.

2. Outline of the thesis

The general aim of this thesis was to investigate the impact of ALAN on predator-prey interactions. Specifically, we examined how ALAN affects the spatio-temporal patterns of activity, behaviours, and visual ecology of predators, which can ultimately alter predation pressures.

I aimed to answer following questions:

- Does ALAN affect the activity patterns of predators and prey?
- Does ALAN affect the spatial distributions of prey and predators?
- Does the impact of ALAN depend on the visual ecology of species?
- Does ALAN alter predation pressures on insect prey?

This work focused on insect prey, as insects occupy a central position in the food web. Insects serve both as prey for higher tropic levels, and affect plants through pollination, herbivory and detritivory (Hassell & May, 1986; Mattson & Addy, 1975; Ollerton et al., 2011; Yang & Gratton, 2014). Alterations in insect communities are therefore likely to have a wide impact on the food web. Current severe insect declines (Hallmann et al., 2017) emphasise the need for a more comprehensive understanding of their challenges, and the development of effective conservation strategies. Insects are impacted by a wide range of stressors, including climate change, chemical pollution, alien species, habitat conversion and fragmentation (Sánchez-Bayo & Wyckhuys, 2019). Although light pollution has only recently been recognised as one of these major stressors, it has the potential to greatly affect insect populations by altering their foraging, movement, reproduction, and susceptibility to predation (Boyes et al., 2021; Grubisic et al., 2018; Owens et al., 2020; van Langevelde et al., 2018).

Throughout the different chapters, I focused on taxonomically diverse predator groups, including avian, arthropod, and mammalian predators. This diversity helped to assess which responses are generalisable and which are more species, or taxa, specific.

In **Chapter 2**, I explored potential changes in caterpillar behaviour under dark and ALAN conditions, which could influence predation rates on these prey. To assess whether and how ALAN would affect species with different adult circadian rhythms and caterpillar anti-predator colourations, I observed the behaviours of three different species: the night-active and cryptic *Mamestra brassicae* (Noctuidae), the day-active and aposematic *Pieris brassicae* (Pieridae), and the day-active, cryptic *Pieris napi (*Pieridae). In this way, I determined how these traits affect the response to ALAN exposure.

In **Chapter 3**, I explored predator-prey behaviours and predation pressure under both dark and ALAN conditions. Given that the nocturnally active, cryptic *M. brassicae* was most affected by ALAN, as established in **Chapter 2**, I subjected this species to predation by the avian predator *Parus major* (Paridae) in a controlled laboratory environment under both dark and ALAN conditions. In addition, to further determine the impact of anti-predator colouration, I conducted a field experiment using artificial dummy caterpillars with different colour patterns, which were placed along dark and ALAN transects.

In **Chapter 4**, I examined how ALAN may influence an arthropod predator: the jumping spider *Marpissa muscosa* (Salticidae). I first investigated the impact of different ALAN conditions on the activity periods of this diurnal species in the absence of prey. I then added prey to examine whether altered activity patterns could lead to nocturnal foraging by this diurnal, visually oriented predator. Since I found that increased nocturnal activity in the spiders was triggered at higher light intensities than those typically found in caterpillar habitats, I used fruit flies instead of caterpillars as prey in this experiment.

In **Chapter 5**, I focused on flying insect prey and bats as mammalian predators to examine how ALAN impacts the spatio-temporal activity patterns of both *Pipistrellus spp.* (Vespertilionidae) bats and flying insects. Bats are known to be highly impacted by light. However, some bat species, including pipistrelle bats, are known to take advantage of light-clustered insects. In this field study, Sander Buddendorf and I investigated whether and how much pipistrelle bats exploited light-attracted insects in highly urbanised settings. We also dimmed streetlights to assess whether dimming light could effectively minimise the disturbance caused by ALAN to both bats and insects. For data collection, we employed interval photography to monitor insect activity, complemented by automated bat recording.

In **Chapter 6**, we validated an open-source object detection model that was trained by Gabriel Charvalakis, whereby we used the manually processed insect data and pictures from **Chapter 5** as an independent validation dataset. This way, we investigated the comparability of manual and automated detection methods and assessed the significance of ambient light conditions and temporal detail for the performance of the model.

Finally, in **Chapter 7**, I integrated all findings to place them in a wider scientific context and synthesised the main implications of my results.

With this work, I aim to advance our scientific understanding on the ecological impacts of ALAN and provide evidence-based insights that can guide conservation strategies to mitigate the harmful effects of ALAN on declining insect populations.

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