

‘Impacts of artificial nighttime light on moths and their food plants’

Submitted by

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Abstract

Over the last 150 years the natural nighttime environment has been drastically altered by the proliferation of artificial light. The amount of artificial light at night is on the increase, and there is a current trend to replace older lighting with more energy efficient types such as light emitting diodes (LEDs) or ceramic metal halide; in Cornwall, UK, there has been a relatively recent replacement of the street lighting, from low pressure sodium to ceramic metal halide. Alongside the increasing amount of artificial nighttime light, recent research has highlighted declines in macro moth numbers. Given the well-known 'flight-to-light' behaviour of moths, and the negative effects this behaviour can have, alongside other known and potential ways in which nighttime light can affect moths, the increasing amount of artificial light in the environment is a suspected contributor to the declines. It is particularly important to understand how modern lighting technologies will impact upon moths, as different spectra of light are known to vary in terms of how attractive they are. As a means to determine the potential impact of different street lighting types on moths, particularly the ceramic metal halide lighting rolled out in Cornwall, UK, we compared the attractiveness to macro moths, of a number of increasingly used, energy efficient, street lighting types. We found that shorter wavelength metal halide lighting attracted significantly more individuals and species of moth than longer wavelength high pressure sodium lighting. In a second experiment, we also found ceramic metal halide lighting to be more attractive to macro moths than LED lighting. Reduced emissions of short wavelength UV light was deemed the likely reason behind the fewer macro moths attracted to the high pressure sodium and LED lighting. Interestingly, we also found striking differences in the relative attractiveness of the

different lighting types to different moth groups. The metal halide lighting attracted significantly more Noctuidae than high pressure sodium lighting, whereas both high pressure sodium and metal halide lighting were equally attractive to Geometridae. Understanding accurately the extent to which different groups of moth are attracted to different wavelengths of light could be useful in determining the impact of artificial light on moth populations.

In addition to impacting moths through attraction, artificial light has the potential to alter the day length as perceived by organisms, which at mid- to high latitudes is utilised by certain species as an abiotic cue to ensure the coincidence of development with favourable environmental conditions. Due to a paucity of knowledge on how raised ambient nighttime light levels affect moths and the trophic levels with which they interact, we carried out analyses into the impact of nighttime light on the winter moth and its host plant oak; a well-studied model system, where synchrony between moth egg hatch and oak budburst is important for the moth's survival. Firstly we carried out an analysis looking at the relationship between the amount of nighttime light and the date of oak budburst. Spatially referenced budburst dates were matched with satellite imagery of nighttime lighting and average spring temperature data, and the relationship between the variables was analysed. Model predictions suggested that oak budburst occurs earlier in brighter areas. In addition, the predicted advance of budburst in brighter areas was still apparent when analysing only the data points that fell outside of large urban areas, where the urban heat island effect is likely reduced. The findings suggested that artificial nighttime light may be causing an advance in oak budburst. To follow up the spatial analysis we carried out a field experiment. We used light cages that simulated various nighttime lighting scenarios to test whether oak budburst and winter moth egg hatch

were affected by low intensity light at night. In contrast to the spatial analysis, there was no significant relationship found between light treatment and the phenology of either oak budburst or winter moth egg hatch. However, there was a suggestion in the data that the higher buds of the oak saplings emerged earlier in the yellow light treatment, highlighting the need for further research into the potential impact of artificial nighttime light on phenology and species interactions.

In conclusion, the findings of this research project provide information useful to those seeking ecologically sensitive lighting solutions, and also highlight a potential tool to assist in determining whether light at night is a causative factor behind apparent moth declines. In addition, they suggest that artificial light at night may be affecting the phenology of an ecological system at a national scale. Finally, this research project has highlighted the complexity of the ecological impacts of artificial light at night, and also a need for further research.

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Author's declaration

Experimental design was a collaborative process between me and my primary supervisors, Richard French-constant, Adrian Spalding, Peter McGregor and David Hodgson. All chapters were drafted by myself, and reviewed by my primary supervisors, who offered advice and made suggestions for improvement. I carried out the majority of the field work and statistical analysis; my supervisor Dave Hodgson assisted me with the statistical analysis. Where contributions were made by others they are outlined on a chapter by chapter basis below; the names of collaborating authors are also listed within the relevant chapters.

Chapter 2

Dave Cruse constructed and wired up the lighting fixtures used for the experiment described in Chapter 2. Mathew Silk assisted with collection and identification of moths from the traps on occasion.

Chapter 3

Fraser Bell, Ben Toulson and Nathan Redman assisted with the data collection for the experiment, and utilised a proportion of the data for their MSc research projects. Therefore some of the data collected and utilised for chapter 3 has already contributed towards a number of MSc dissertations previously submitted to the University Of Exeter; additional data was collected and analysed for the experiment described in Chapter 3.

Chapter 4

Chapter 4 involved analyses of data collected by citizen scientists as part of the Woodland Trust's 'Nature's Calendar' programme, satellite imagery of nighttime light, and temperature data from the met office. Jon Bennie calibrated the satellite imagery

of nighttime lights, used in the analyses, to improve accuracy; he also reviewed the manuscript. Theodoros Economou reviewed my statistical analysis and assisted me with the general additive modelling.

Chapter 5

The design of the light cages used for chapter 5 was informed by some similar light cages used for experiments carried out as part of the 'Ecolight' project at the University of Exeter. Dave Cruse assisted me with the construction and wiring of the light cages. Oak saplings were provided by the Devon based charity, 'Moor Trees'. Winter moth ova used in the experiment were provided by Lucia Salis at Wageningen University.

Annexed documents

The annexed documents are publications stemming from the data chapters 2 and 4; they have been included to highlight that the work has contributed towards peer reviewed publications. Annex 1 is very similar to chapter 2 and my contribution to it is the same. However, annex 2 differs from chapter 4, as does my contribution. The analysis of oak budburst carried out in chapter 4 was repeated for an additional three tree species; Jon Bennie repeated the analysis, used in chapter 4, for the additional tree species, and he also, alongside the other co-authors, altered the text of the document accordingly; I made less of a contribution to these changes.

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Chapter1: A review and introduction; the ecological impact of light pollution on moths.

Light pollution

For millions of years, prior to the development of artificial light, Earth and the organisms upon it have been subject to natural cycles of light and dark governed by Earth's rotation and orbit, with light from solar, lunar, and celestial sources. Given the length of time most organisms have had to evolve under these natural day/night cycles, it is unsurprising that the ambient light level plays an extremely important role in natural systems; it acts as both a resource and abiotic cue, driving many biological phenomena, from physiological processes to daily and seasonal patterns in the activity of many organisms activity (Gaston *et al.* 2012; Arendt 1998; Smith 2000). Over the last hundred and fifty years or so, the natural nighttime environment has been drastically altered by the proliferation of artificial light. Such artificial light comes from a number of sources including street lighting, domestic lighting, security lighting, advertising lighting, architectural lighting and vehicle lighting (Gaston *et al.* 2015). Artificial nighttime light alters natural lighting patterns either directly from the aforementioned sources, or indirectly through a phenomenon known as skyglow. Skyglow is a diffuse light caused when direct or reflected sources of artificial nighttime light are scattered throughout the atmosphere by water, dust and gas molecules (Gaston *et al.* 2014). One study looking at satellite imagery of earth at night, came up with an estimate that 11.4% of terrestrial and 0.2% of marine areas of the globe experience artificial light at night (Gaston *et al.* 2014), whilst another study in 2001, accounting for the effects of skyglow, came up with an estimate that almost one fifth of the Earth's land surface was above a light level deemed polluted

(Cinzano *et al.* 2001). In addition, global artificial light emission has been estimated to be increasing at a rate of about 6% annually (Hölker *et al.* 2010), although trends in the amount of light pollution are spatially heterogeneous and in some economically developed areas observed night sky brightness apparently decreased over recent times (Bennie *et al.* 2014).

Given the known importance of light to natural systems, the increasingly large amount of artificial light in the environment, and already documented impacts of artificial light on living systems (see Gaston *et al.* 2013; Longcore & Rich 2004; Navara & Nelson 2007 for reviews across all taxa) it is unsurprising that the ecological impacts of artificial light are of increasing concern.

Moths

One of the most conspicuous and well known impacts of artificial light on living organisms is demonstrated by the 'flight-to-light' behaviour of moths. Many different organisms display 'flight-to-light' behaviour/positive phototaxis, from birds to insects (Jones & Francis 2003; Eisenbeis 2006), and it is in part due to this behaviour that the potential impacts of artificial nighttime lighting on moths are of concern. They are also of concern because moth populations in Britain and in other parts of Europe are known to be declining (Fox *et al.* 2013; Conrad *et al.* 2006; Groenendijk & Ellis 2010; Mattila *et al.* 2006; Mattila *et al.* 2008). A 40 year study in Britain, of 337 common and widespread macro moth species, showed that between 1968 and 2007, total moth abundance decreased by 28%; the change was more marked in the southern part of Britain than in the north. Although this decline is deemed likely to be driven predominantly by habitat degradation and climate change (Fox *et al.* 2014), artificial nighttime lighting is thought to be a potential contributing factor (Fox *et al.* 2013).

Aside from the intrinsic value of moths, they play an ecologically important role as a food source to higher trophic levels such as bats (Jones 2016), and are increasingly being recognised for their role in pollination (Devoto *et al.* 2011; MacGregor *et al.* 2015); pollination is an essential ecosystem service and declines in pollinators have been linked with declines in the plants they pollinate (Potts *et al.* 2010; MacGregor *et al.* 2015). Given the important role of moths as part of the wider ecosystem, it is important to understand how they may be impacted by the increasing amount of artificial light at night. The aim of this introduction is to outline the already established impacts artificial light at night has upon moths, as well as to highlight some of the less established but potential ways in which it could do so, as a means to put into context and justify the proceeding experimental chapters.

'Flight-to-light' behaviour

There are a number of suggested theories as to why moths fly towards light. One of the most well-known theories suggests that moths navigate by flying at a constant angle to the moon, and that they mistake artificial light sources for the moon; where the moon is so distant it stays in the same relative position despite the moths' flight, the position of a nearby artificial light source changes with the moths flight, resulting in a spiralled flight towards the light source (Baker & Sadovy 1978). The mach band theory suggests that areas of relative darkness are made apparent immediately adjacent to a light source, and that moths fly towards these areas of darkness (Hsiao 1972). Another theory suggests that moths fly towards artificial light because their vision is impaired by it to the point where all they can see is the artificial light (Hamdorf & Høglund 1981). Although there is some fairly convincing experimental evidence in support of moths mistaking artificial light sources for the moon, and thus being attracted to such light sources (Sotthibandhu & Baker 1979), there is such

variation in the behaviour of moths around artificial light sources (Frank 2006), that no one theory alone is entirely conclusive.

Impacts/potential impacts of artificial light at night on moths

What all the aforementioned theories on 'flight-to-light' behaviour have in common is a lack of benefit to moths; this suggests that at the very least, 'flight-to-light' behaviour in and of itself is of detriment to moths because whilst they are doing it they are not carrying out their natural necessary activities such as feeding and mating. Even a short time at an artificial light source whilst not carrying out other necessary activities could be a high cost to a moth, as they are sometimes only active for part of the night, and only live for relatively short periods of time (Frank 2006). A study by (Macgregor *et al.* 2016) showed that moth activity is reduced by half at ground level in lit sites compared to equivalent unlit sites, whilst overhead flight activity was found to be 1.7 times higher at lit sites compared to unlit sites. The known and potential impacts of artificial nighttime lighting not only manifest themselves as a direct consequence of positive phototaxis/'flight-to-light' behaviour however. In addition, heightened ambient light levels caused by artificial light sources can also affect moths in various ways. This is of particular concern when considering the large areas of earth experiencing artificially heightened light intensities caused by skyglow, and the fact that very low light intensities are known to affect certain biological processes (Nemec 1971). Whilst the action of flying to light it is potentially a disruption to a moth's natural activities, some moths that have approached a light settle down and become inactive (Wolfling *et al.* 2016). Moths that have settled in proximity to artificial light sources can do so for hours, or the remainder of the night (Janzen 1984). It is possible that the moths perceive the artificial light as daylight and thus behave as if it is the day time, indeed, Frank

(2006) suggests that such inactivity for long periods of time could indicate that artificially heightened light levels reset the circadian clock that regulates the flight in moths. Such suppression of activity could potentially be triggered by very low light levels; corn earworm moth (*Helicoverpa zea*) activity was shown to be suppressed by light intensities of as low as 0.1 lux, less than a fifth of the brightness of full moonlight (Nemec 1971).

Vision

As mentioned in one of the previously described theories of why moths exhibit positive phototaxis, moths' vision can be affected by artificial light. The compound eyes of the elephant hawk moth (*Deilephila elpenor*) adapt to increases in light level through the movement of screening pigment; a short exposure to light can quickly trigger the movement of these pigments, reducing their ocular sensitivity (Hamdorf & Hoglund 1981). The return to full ocular sensitivity can take a lot longer according to a study on another species of moth (Bernhard & Ottoson 1960). The previous experiments weren't carried out in the field, but show that artificial night lighting in natural conditions has the potential to affect the vision of moths, which may have knock on consequences for the survival of moths. In addition, artificial light at night could potentially have indirect effects upon the vision of moths. Moths can use their visual ability to locate nectar sources/flowers; some flowers have UV markers, known as nectar guides, which help insects visually sensitive to UV, such as moths, to locate them (Barth 1985). Artificial light at night could potentially affect the ability of moths to detect nectar sources (Davies *et al.* 2013). UV rich sources of artificial night lighting, could accentuate such UV markers, whereas light sources that don't emit UV light could have the opposite effect, highlighting other neighbouring features thus making nectar sources less visible (Frank 2006). Whether due to 'flight-to-light'

behaviour in and of itself, suppression of flight, impaired vision, or heightened ambient light levels, the potential impacts of artificial nighttime lighting on moths are many.

Direct mortality at artificial light

Moths attracted to artificial light sources can suffer direct mortality when they come into contact with the hot components of a light source, they can also get trapped inside lamp housings and damage themselves whilst flying into and around a light source (Frank 2006).

Predation at artificial light

In addition to mortality caused by artificial light sources themselves, moths attracted to artificial light can also expose themselves to increased predation risk. Certain species of bat are known to prey upon moths and other insects that have been attracted to artificial light sources (Rydell 1992). Predatory insects such as wasps are also known to prey upon moths at artificial light (Warren 1990). Spiders are known to build webs in illuminated areas rather than darker areas as doing so enables them to capture more prey (Heiling 1999), and amphibians and reptiles prey upon insects in artificially lit areas (Henderson & Powell 2001). Not only are moths exposed to increased predation by bats around street lighting, certain species of moth are also less able to evade the predatory bats. Under normal circumstances tympanate moths have the capacity to hear echolocating bats and are known to perform evasive manoeuvres to avoid being preyed upon. However, both LED and mercury vapour street lighting have been shown to interfere with this defensive capability, with evasive manoeuvres by moths markedly reduced when in proximity to the street lighting (Svensson & Rydell 1998; Wakefield *et al.* 2015). Many moths are cryptically coloured as a means to blend into their surroundings and avoid

predation. If moths that are attracted to artificial light sources alight on unsuitable locations where their wing patterns are not well camouflaged then they may be more susceptible to predation. In addition, if their numbers are concentrated into smaller areas at artificially lit sites then predators may be more quickly able learn to recognise the moths camouflage (Frank 2006). Similarly, increased concentrations around artificial light sources of moths with aposematic colouration could increase their risk of being preyed upon; over time, predators can become habituated to startling displays (Ingalls 1993), and increased exposure to such displays could potentially accelerate this process (Frank 2006). The fact that moths vision can also be detrimentally affected by artificial light at night (Hamdorf & Hoglund 1981) may also make them more susceptible to predation around a light source.

Feeding

Recent experiments suggest that artificial light may disrupt pollen transport, as moths in lit areas are less likely to carry pollen than those at unlit sites (Macgregor *et al.* 2016); as the main reason for adult moths to visit flowers is to feed on nectar (Willmer 2011), this result may also suggest that moths' feeding is disrupted by artificial nighttime lighting. However, some moths have been observed to feed in the direct vicinity of artificial light sources (Frank 2006). Disruption to feeding could potentially be caused by artificial light obscuring the visibility of flowers, or it could be disrupted by the previously mentioned suppression of flight by artificial light, or by 'flight-to-light' behaviour itself.

Reproduction

Experiments in the Netherlands have revealed how artificial light of varying colours can inhibit mating in the winter moth (*Operophtera brumata*); they showed that fewer flightless females were found on illuminated trunks of trees, where they mate, than

on non-illuminated trunks, and also that those females found on illuminated trunks were less likely to have mated than those found on non-illuminated trunks. In a second experiment, the same authors showed that artificial light reduced the number of male moths attracted to synthetic pheromone lures; they found this effect to be strongest under red light and milder under green light (van Geffen *et al.* 2015). Another experiment showed how low levels of artificial light, regardless of colour, can simultaneously reduce the amount and composition of sex pheromones produced by female cabbage moths (*Mamestra brassicae*); this could potentially reduce the attractiveness of the pheromones to male moths, with consequences for reproduction (van Geffen *et al.* 2015). In addition, oviposition by *Heliothis* species moths has been observed to be reduced under illuminated conditions compared to unlit conditions (Nemec 1969). Conversely, certain moth species have been observed to oviposit on buildings near to artificial lights, and infestation of certain pest moths has been observed to be greater in close proximity to artificial light than further away (Pfrimmer *et al.* 1955; Brown 1984). Such effects of artificial nighttime light on reproduction could have consequences for moth populations, and may contribute towards the previously mentioned observed moth declines.

Migration

Artificial light at night may also disrupt the dispersal and migration of moths. Certain species of migrating moths have been observed to fly to artificial light sources located at large distances from any suitable breeding habitat, such as lighting on offshore oil platforms (See (Frank 2006) and other references therein for a summary).

Artificial alteration of photoperiod

As previously mentioned, it is possible that nocturnal moths in the vicinity of artificial nighttime light may be fooled into thinking that it is in fact the day time and become inactive accordingly. It is also possible that the day length, as perceived by moths or their host plants, is altered by artificial light at night. For many organisms, the photoperiod or day length plays a role as an abiotic cue, organising seasonal patterns in their activity (Gaston *et al.* 2013). At mid to high latitudes changes in the day length are perceived by many organisms and utilised as a cue to prompt the onset or postponement of their development to ensure coincidence with appropriate environmental conditions. For example a number of moth caterpillars use shortened day length as a cue to trigger the onset of pupal diapause; diapause is a temporary and reversible state of physiological dormancy/suspended development, often used during periods of unfavourable environmental conditions (Xiao *et al.* 2010; Adkisson 1966). This ensures that late generation caterpillars or pupae over winter in diapause, thus ensuring their adult life stage coincides with favourable spring conditions (Adkisson 1966). Low levels of artificial light at night have been shown to reduce the duration of pupation in the cabbage moth, and the authors deemed this likely due to inhibition of diapause caused by artificial night lighting (van Geffen *et al.* 2014). The same study showed that male caterpillars subjected to green and white light at night reached a lower maximum mass, pupated earlier and obtained a lower pupal mass than male caterpillars in the dark control or under red light. Such a result has potential consequences for the moth's fitness and as such for moth populations. For many organisms, including moth species, the timing of seasonal events, such as egg hatch or pupation, is extremely important, and the optimal period for the occurrence of such events is not always governed entirely by abiotic conditions;

often it is governed in part by species at underlying trophic levels (Visser & Holleman 2001). For example, the winter moth (*Operophtera brumata*) needs to time its egg hatch so that it coincides with the emergence of their food plant oak buds (Visser & Holleman 2001; Buse *et al.* 1999; Buse & Good 1996). Vascular plants, such as the winter moths' food plant oak, are able to utilise phytochrome photoreceptors to effectively determine the day length, and this ability can assist them in timing key phenological events such as bud burst (Basler & Körner 2012; Gaston *et al.* 2013; Smith 2000). As such, plants could also potentially perceive changes in day length due to artificial light at night; indeed artificial light at night has been known to affect the phenology of certain plants (Matzke 1936; Bennie *et al.* 2016). Whilst moths and their host plants have evolved together and as such might be expected to respond to natural environmental cues similarly, this is not necessarily the case for novel artificial stimuli such as nighttime light, which up until relatively recently would not have been experienced by either moth or host. Therefore artificial light at night has the potential to knock moths and their host plants out of phenological synchrony, and this could have negative consequences for moth populations, particularly specialist monophagous species with only a short period of time during which their host plant is available.

Differences in 'flight-to-light' behaviour among moths

Interestingly, male moths may be more likely to experience some of the aforementioned negative consequences of artificial nighttime lighting. Male biased 'flight-to-light' behaviour has been observed in some species of moth, although it is unclear as to whether this is due to the fact that male moths are more attracted to light or whether they are just generally more aerially active than female moths and so more likely to encounter and thus be attracted to artificial light sources (Altermatt *et*

al. 2009). The authors of the previously cited study suggest that male biased 'flight-to-light' behaviour may influence dispersal rates and connectivity of moth populations, as males often tend to disperse more than females, creating gene flow between populations. They state that if increased flight activity increases the likelihood of flying to light, then there will be a selection pressure against active and mobile individuals.

As well as differences in 'flight-to-light' behaviour between sexes of moth, different species of moth also behave differently around artificial light sources. Some species of moth are deemed far less likely than others to be attracted to artificial light (See (Frank 2006) and other references therein). In addition, small moths have been shown to be more likely to settle down and remain stationary at light traps than larger moths (Wolfling *et al.* 2016), whilst larger moth species are generally considered to be more attracted to shorter wavelength light than smaller moths. This suggests that the previously described impacts of 'flight-to-light' behaviour may vary between species. Variation between insects attracted to artificial light sources is also dependent on the spectra of the light source in question, different orders and families of insect are known to vary in terms of the spectra of light they are attracted to; see (Longcore *et al.* 2015) for a summary, and see chapter 2.

Impact of lighting characteristics on ecological impacts

All of the previously described ecological impacts and potential impacts of artificial light are in turn influenced by the characteristics of the artificial light sources in question. Both the intensity of artificial light and its spectral quality, in terms of the frequency of emitted wavelengths, have long be known to influence how attractive a light source is to moths and other insects, and it is also becoming clear that such

lighting characteristics also make a difference to ecological impacts other than light attraction itself (van Geffen *et al.* 2015).

With regards to phototaxis, bright light, with shorter wavelengths and higher UV content, is generally more attractive (Barghini & De Medeiros 2012; Eisenbeis 2006; Kolligs 2000; Eisenbeis & Eick 2011; Rydell 1992; van Langevelde *et al.* 2011; Bowden 1982; van Grunsven *et al.* 2014). However, as previously mentioned, how attractive a light source is to an insect can depend on the insect in question; different orders and families of insect are known to respond differently to different lighting types (Longcore *et al.* 2015) (see chapter 2). The attractiveness of a light source can also be affected by a number of other factors such as its height (R. Baker & Sadovy 1978), and the relative background illumination; attraction to a light source appears to be reduced when there is increased amounts of competing background lighting, be it from artificial or natural sources (Bowden 1982; Robinson & Robinson 1950; Frank 2006). How attractive a light source is, is generally measured by how many insects or moths fly to it; and this in turn is likely influenced by variation in the distance from which moths are compelled to fly to a light source. Various estimates of distances from which moths are attracted to artificial light sources have been made, and the distances vary greatly. Baker & Sadovy (1978) found that the attractive range of a 125W mercury vapour lamp was only 3m for two species of noctuid moth, and Truxa and Fiedler (2012) also estimate that moths are attracted from only a short distances. In addition, Merckx and Slade (Merckx & Slade 2014) estimated that certain moths are attracted from between 10m and 27m to low wattage actinic light traps, depending on their family. Kolligs (2000), on the other hand found that moths were attracted from up to 130m, and even greater distances of attraction have been estimated based on the retinal sensitivity of moths (See

(Frank 2006; Bowden 1982) and references therein). Such variation is unsurprising considering the different methodologies used, known variation between the attractiveness of different light sources, and variation amongst moths in terms of their attraction to light (van Langevelde *et al.* 2011).

Long term and community level impacts of light pollution

The most well-known and well documented consequences of artificial light on moths have to do with the immediate detrimental impacts of their 'flight-to-light' behaviour. There are also an increasing number of studies highlighting impacts of artificial light on other moth behaviours, their physiology and life histories. However, although artificial light at night does have the potential to alter invertebrate communities (Davies *et al.* 2012), studies focussed on the impacts of artificial light on moth communities are limited. In addition, there are only few studies looking at the longer term effects of artificial night lighting on moths, or how the known impacts of artificial light at night will go on to affect their populations. A study comparing the 'flight-to-light' behaviour of moths from urban populations with those from pristine populations found that the urban moths had a reduced attraction to artificial light, and whilst the authors concluded that this is likely an evolutionary adaptation that may have benefits, such as increased survival and reproduction, they also anticipate that such an adaptation will come at a cost, in the form of reduced mobility and ability to colonize new areas. They also suggest that an evolutionary change in the 'flight-to-light' behaviour of moths will potentially cascade across species interaction networks (Altermatt & Ebert 2016). In the Netherlands a large scale, ecosystem wide study is currently underway, looking into the effects of various types of artificial night lighting. Although the experiment has already highlighted community level effects on birds, no effects on moth populations have yet been observed; however, the researchers

anticipate that these effects may become apparent after a longer period of time (Spoelstra *et al.* 2015).

The future

Artificial night lighting is a major part of, and convenience to, modern society, and is often perceived to make the nighttime environment a safer place for humans to remain active for longer (there is however, limited scientific evidence to support such a perception). As such, it is likely that reducing the ecological impacts of night lighting as opposed to completely removing them will be the only option, especially given that most types of modern artificial light, in terms of spectra and intensity, are known to or have the potential to affect at least some type of organism (Longcore *et al.* 2015; Nemeč 1971; van Geffen *et al.* 2015). There is a current general trend to replace older lighting types with more energy efficient types such as light emitting diodes (LEDs)(Longcore *et al.* 2015), or ceramic metal halide lighting in certain cases, and it is important to know how such changes in night lighting will affect ecological systems. One of the largest sources of artificial light at night is street lighting (Luginbuhl *et al.* 2009), so it is of particular importance to know how different street lighting technologies will impact upon the natural environment. A number of studies have looked into the impacts of different lighting types on moths and other insects (Wakefield *et al.* 2015; Eisenbeis 2006; Eisenbeis & Eick 2011; van Grunsven *et al.* 2014; Longcore *et al.* 2015; Pawson & Bader 2014), most of which compare lighting types in terms of their attractiveness to the insects. Five of the previously cited studies look at LED lighting, and one study looks at ceramic metal halide lighting; the findings of most of these studies conform to the fact that lighting types that emit less short wavelength and UV light attract fewer insects. The findings of the experiments looking at LEDs have been mixed; whilst most of the studies

found LEDs to be generally less attractive to insects and moths, one study found that LED lighting attracted more insects than high pressure sodium lighting (Pawson & Bader 2014). Generally speaking, LEDs tend not to emit UV light, and are thus considered likely to be less attractive to insects and moths than narrower spectrum, older lighting types. However, due to the broad spectrum of light, and particularly the blue light, emitted by LEDs, they are considered potentially more problematic for ecology in other ways, than narrower spectrum, older lighting, that lacks such blue emissions (Pawson & Bader 2014; Longcore *et al.* 2015; Davies *et al.* 2013; Gaston *et al.* 2013). Fortunately, it is possible to produce white light from LEDs in multiple ways, and experiments manipulating the spectrum of white LED light have managed to reduce the attractiveness of a light source to insects whilst maintaining the same colour temperature (Longcore *et al.* 2015). Ceramic metal halide lighting is also a broad spectrum white lighting, but is considered likely to have a greater ecological impact than LED lighting because it does emit some light in the UV (van Grunsven *et al.* 2014).

Scope of experimental chapters

The preceding literature review has highlighted a number of potential areas of research that would better the understanding of the impacts of artificial nighttime lighting on moths; in particular there is a lack of understanding as to how artificial light at night will affect moth populations as a whole, as well as the communities they are part of. There is also a notable lack of research into how artificial light at night affects moths host plants, which is important because impacts upon host plants could have knock-on effects on moths and other higher trophic levels. In addition, the rapidly changing nighttime light environment and developments in technology highlight the need to understand the impact of emerging, energy efficient lighting

types. Specifically, given the locality of the current research project (Cornwall, UK), a focus on ceramic metal halide lighting technology is necessary. In 2009, Cornwall County Council began to replace existing low-pressure sodium (LPS) street lighting with new Phillips CosmoPolis white ceramic metal halide street lights to reduce energy usage.

Chapter 2 focuses upon the relative attractiveness of two lighting types to macro moths; one already common and widespread type, high pressure sodium, which is increasingly being phased out by more energy efficient lighting technologies, and one more modern lighting type which will potentially become more widespread, as it is an energy efficient alternative, metal halide. This experiment was carried out because the rollout of ceramic metal halide street lighting in Cornwall is, in part, what inspired the whole PhD project. In addition, although there are a number of experiments that have compared lighting types in terms of their attractiveness to moths, fewer have looked specifically at street lighting, and knowledge on the subject is far from extensive. Further experimentation comparing lighting types is potentially valuable, particularly given the focus on new energy efficient lighting technologies.

Similarly, chapter 3 also summarises an experimental comparison of the attractiveness of two street lighting types to macro moths (LED and ceramic metal halide). The justification for carrying out this experiment is much the same as for chapter 2, but additionally, contrasting results of other similar studies and the likely proliferation of LED lighting make this particularly valuable.

As was previously highlighted, there is a lack of research into how artificial light at night affects moths host plants, and in turn, interactions between moth and host.

Chapters 4 and 5 are prompted by this knowledge gap.

Chapter 4 summarises an analysis of the spatial relationship between oak budburst phenology and the amount of night light, using citizen science data on oak budburst and satellite imagery of light at night spanning thirteen years.

Chapter 5 summarises an experiment looking into the effect of different colours of low intensity light upon the timing of oak budburst and winter moth egg hatch, and thus investigates a potential way in which artificial light could disrupt species interactions.

Measuring light

In the subsequent experimental chapters, various measures of light are presented; a brief description of the various ways in which light can be measured will be detailed here, in order to support what is later mentioned in the thesis. Radiometry is the measurement of the optical portion of the electromagnetic spectrum; it includes the measurement of ultraviolet, visible and infrared light. Photometry is similar to radiometry, only measurements are scaled by the spectral response of the human eye. Radiometric power/radiant flux is measured in watts (W), while photometric power/luminous flux is measured in lumens (lm). Another commonly used photometric unit of measurement is lm/m^2 (lux); lux is the measure of illuminance (Palmer 2003). Both lux and lumens are reported in the subsequent chapters, as a means to compare different light sources being used in the experiments; these are useful measures for comparing the functionality of street lighting types, in terms of how bright they are likely to appear from a human perspective. However, it is worth noting that just because one light source may appear brighter to a human than another light source, does not mean it will appear that way to an insect; insects are visually sensitive to UV light (Briscoe & Chittka 2001) whilst humans are not, so a UV light might appear very bright to an insect whilst invisible to a human. It is also worth

noting that the intensity of light experienced by an organism varies depending on the distance from the light source; light intensity is inversely proportional to the square of the distance from the source. It is therefore difficult to know what light intensity will be experienced by organisms that are exposed to artificial light sources, and thus what intensity of light actually elicits a response such as 'flight-to-light' behavior.

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Chapter 2: Shedding light on moths: shorter wavelengths attract noctuids more than geometrids.

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Abstract

With moth declines reported across Europe, and parallel changes in the amount and spectra of street lighting, it is important to understand exactly how artificial lights affect moth populations. We therefore compared the relative attractiveness of shorter wavelength (SW) and longer wavelength (LW) lighting to macro moths. SW light attracted significantly more individuals and species of moth, either when used alone or in competition with LW lighting. We also found striking differences in the relative attractiveness of different wavelengths to different moth groups. SW lighting attracted significantly more Noctuidae than LW, whereas both lighting types were equally attractive to Geometridae. Understanding the extent to which different groups of moth are attracted to different wavelengths of light will be useful in determining the impact of artificial light on moth populations.

Introduction

Much of the world is artificially illuminated at night (Cinzano *et al.* 2001) and global artificial light emission has been estimated to be increasing by ~6% annually (Hölker *et al.* 2010). This increase is accompanied by changes in the abundance of nocturnal Lepidoptera. Recent analyses have highlighted declines in the populations of larger (macro) moths in the United Kingdom and Europe, with population trends varying among species (Conrad *et al.* 2006; Groenendijk & Ellis 2010; Mattila *et al.* 2006; Mattila *et al.* 2008; Fox *et al.* 2013). These declines are likely due to a combination of factors, including habitat loss and anthropogenic climate change (Fox 2012). Another suspected driver, however, is light pollution (Conrad *et al.* 2006; Groenendijk & Ellis 2010; Fox 2012). Two of the largest sources of artificial light are street lighting and sports fields (Luginbuhl *et al.* 2009), and studies have shown that different types of widely used light vary with regards to how many insects they attract; light with shorter wavelengths and higher UV content is generally more attractive (Rydell 1992; Eisenbeis 2006; van Langevelde *et al.* 2011; Kolligs 2000; Eisenbeis & Eick 2011; Barghini & De Medeiros 2012). Artificial light has the potential to affect moths in many ways, including disrupting their foraging, dispersal, breeding and inter-specific interactions (Frank 2006; Altermatt *et al.* 2009), as well as increasing their risk of predation (Rydell 1992; Svensson & Rydell 1998). However, what specific impact artificial light has on different groups of macro-moths is largely unknown.

Given the important role insects play in ecosystem functioning (Fox 2012), it is important to determine whether artificial light is having an impact on moths at the population level. Further, an understanding of the different degree to which moth families or species are attracted to different types of widely used lighting will be useful in trying to determine whether artificial lighting is contributing to the decline of

specific groups. To address this need, here we compare the attractiveness of shorter and longer wavelength lights to UK moth populations across a full field season.

Material & Methods

Study area and lighting

Experiments were performed in the Walled Garden. Tremough Campus, Penryn, England (grid reference SW76975 34609) between 26/06/2012 and 10/10/2012. The site was chosen as it is representative of the suburban habitats in the UK likely to be affected by street lighting. To compare lights of longer and shorter wavelength, four lamppost structures were mounted on a wall overlooking the site. From each of the lamppost structures were suspended two adjacent lights, a high-pressure sodium floodlight (150 Watt, 15000lm, FL150SON/L) characterised by yellowish 'longer wavelength' light and hereafter termed 'LW', and a metal halide floodlight (150 Watt, 12000lm, FL150HQI/C) characterised by 'shorter wavelength' white light or 'SW' (see figure 2.1 and figures A2.1 and A2.2 in appendices 2). Lighting type was selected on each lamppost with a switch. The lampposts were positioned ~14.5m apart and the lights were angled at approximately 45°. The average total height of the lights was 5.65 ± 0.13 s.d. m, although they remained only 3.1 ± 0.33 s.d. m above the ground from behind the wall (see figure A2.2 in appendices 2).

Lights alone or in competition

It has been suggested that moths only exhibit a phototactic preference to certain lighting types under conditions of light 'competition', where two or more lighting types are operated simultaneously in close proximity (Scheibe 2000). Although a previous study found results contrary to this idea (Eisenbeis 2006), we investigated this hypothesis by testing the SW and LW lighting either alone (only SW or LW lights on

all night) or in competition (SW and LW lighting alternating along the same transect). On any given night, both types of light (LW and SW) were alternated along the four lampposts in direct competition with each other. The order of the alternation was then changed on each consecutive night of trapping so as to control for the variation caused by the position of each of the lampposts. In the second, non-competitive configuration on any given night, all of the lampposts displayed the same lighting type. The lighting type was alternated on consecutive nights of trapping. For both experimental configurations, lights were turned on and off automatically by a photocell. Macro moths were trapped with safari moth traps suspended below each of the lights. A standardised number of seedling trays were used within the traps as refuge for the moths (see figure A2.2 in appendices 2). The traps were checked at ~8:30 am every morning. Moths were collected live and identified to species level where possible. Moth identification took place at the site, and identified individuals were released in situ (see appendices 2 for justification of in situ release and removal of certain species for identification).

Statistical analyses

Competitive configuration.

For the data collected from the competitive lighting configuration, the relationship between lighting type and overall moth abundance was analysed using a generalised linear mixed effects model (glmm) with a negative binomial error structure; a negative binomial error structure was used to account for the overdispersion of the count data. Moth abundance was incorporated into the model as the response variable, with lighting type as the explanatory variable. To account for any daily variation in moth abundance caused by changing environmental conditions, and variation caused by the position of the traps, date of trapping moment and lamppost

position were incorporated into the model as random effects. The glmm analysis was carried out using the 'glmmADMB' package (v. 0.7.2.12) (Skaug *et al.*, 2013).

Non-competitive configuration.

To avoid violating any assumptions of independence, data collected from the non-competitive lighting configuration was pooled into nightly totals. A generalised linear model with poisson error structure was used to test for differences in overall moth abundance between the two lighting types; moth abundance was incorporated into the model as the response variable and lighting type as the explanatory variable. To account for the influence of environmental conditions on moth abundance, daily averages of temperature (°C), rainfall (mm), wind speed (km/h) and lunar phase (% of moon visible) for the day prior to the morning of moth collection, were incorporated into the models as covariates (weather data was obtained from a weather station at a site ~13km from the study area, via the 'Weather Underground' website <https://www.wunderground.com>). This analysis was repeated separately for the two most abundant moth families and species. The overall species richness of the moths attracted to the two lighting types in the non-competitive lighting configuration was also compared using the same statistical technique. In cases where the count data being analysed was found to be overdispersed, a negative binomial error structure was used rather than the Poisson error structure. Tests of significance were carried out with likelihood ratio tests, comparing null models with alternative models. The Poisson models were constructed using the 'glm' function from the base package 'stats', whilst the negative binomial models were constructed using the 'glm.nb' function from the MASS package (version 7.3-18); tests for overdispersion were carried out using the 'dispersiontest' function from the AER package (version 1.2-2). The relationship between overall moth abundance and species richness was tested

using Spearman's correlation coefficient. Model selection was based on comparative model check plots of residual versus fitted values, and checks of normality of the residuals. All statistical analyses were carried out using R x 64 2.15.1 (R Core Team, 2012).

Results

SW lighting attracted significantly more individuals than the LW lighting in both configurations (non-competitive, 'glm.nb': *Likelihood ratio statistic*₁ = 7.96, $p = 0.005$, $n=40$; competitive, 'glmmADMB': $\chi^2_1 = 12.2$, $p < 0.001$, $n=56$, figure 2.2 (a) & (b)), with a catch ratio of SW:LW of about 2:1 (competitive 2.13 : 1; non-competitive 1.91 :1). Also, significantly more species were attracted to SW than LW lighting (non-competitive, 'glm.nb': *Likelihood ratio statistic*₁ = 7.26, $p = 0.007$, $n=40$, figure 2.3). The number of species caught was positively correlated with the number of individuals caught (non-competitive, Spearman correlation coefficient $r_s = 0.96$, $p < 0.001$, $n=40$). However, the two most commonly caught moth families responded to lighting differently (figure 2.4 (a) & (b)); significantly more noctuids were attracted to the SW lighting than the LW lighting (non-competitive, 'glm.nb': *Likelihood ratio statistic*₁ = 10.72, $p = 0.001$, $n = 40$), but geometrids showed no significant difference (non-competitive, 'glm': $\chi^2_1 = 0.0001158$, $p = 0.99$, $n = 40$). The two most commonly caught species, both noctuids, also responded to lighting differently (figure 2.5 (a) & (b)). Significantly more *Ochropleura plecta* were attracted to the SW than the LW lighting (non-competitive, 'glm.nb': *Likelihood ratio statistic*₁ = 7.97, $p = 0.005$, $n = 40$), whilst there was no significant difference between the numbers of *Noctua janthe* (non-competitive, 'glm.nb': *Likelihood ratio statistic*₁ = 2.63, $p = 0.1$, $n = 40$).

Observation of the raw data suggests that further species may differ in terms of the

degree to which they are attracted to the two lighting types (figure 2.6); further analysis would be required to confirm this.

Discussion

The results illustrate that the SW lighting attracts both greater numbers of species and individuals of moth than LW, attracting higher numbers of individuals whether the lighting types are in direct competition with each other or not (figure 2.2 (a) & (b)). Catch ratios were similar, with the LW lighting attracting ~53% fewer moths in the competitive lighting configuration and ~ 48% fewer in the non-competitive configuration. This result agrees with that of Eisenbeiss (Eisenbeis 2006), and contradicts Scheibe's hypothesis that moths only exhibit a phototactic preference for certain lighting types under conditions of light competition (Scheibe 2000). Previous studies have shown that shorter wavelength light, and particularly UV light is more attractive to insects (Eisenbeis 2006; van Langevelde *et al.* 2011; Barghini & De Medeiros 2012) , however, further analysis of the two most numerous moth families illustrated that the difference in abundance of moths attracted to the two lighting types was driven predominantly by differences in the numbers of noctuids and there was no significant difference between the numbers of geometrids. The precise reason behind this unclear, but it could be due to the higher sensitivity of geometrids to light of 597 nm (see (van Langevelde *et al.* 2011)), as the LW lighting used in this investigation emits more light of 597 nm than SW (figure 2.1). Alternatively, noctuids may be particularly attracted to the increased amounts of UV light emitted from SW, possibly mistaking the UV emission for a nectar source (Penny 1983). There are also indications that individual species differ between SW and LW (figure 2.5 & figure 2.6). The two most abundant species, *Noctua janthe* and *Ochropleura plecta*, differed in terms of the degree to which they were attracted to the two lights (figure

2.5), and observation of the raw data suggest that this may also be the case with other species (figure 2.6); *Noctua pronuba* appears markedly more attracted to shorter wavelength light than longer wavelength light, whilst *Miltochrista miniata* appears equally attracted to both lighting types. Further experimentation would be needed to investigate the differences between species, in terms of how attracted they are to two different light sources, as the amount of data available for the current analysis was relatively low. More research, further quantifying the degree to which moth families or species differ in terms of their attraction to wavelengths of light, and into the physiological or life history traits that determine the different degrees of attraction, will be useful in assessing the impact of artificial light on moths. Assuming that increased attraction to light results in increased moth mortality, one might expect noctuid populations to decline more steeply in areas where the predominant source of artificial light emits more shorter wavelength and UV than in areas where the light emits less UV and more longer wavelength light, whereas geometrids would likely be similarly affected in both areas. Interestingly, of the 61 species of British macro moth that have declined by 75% or more in recent years, 35 are Noctuidae compared to only 19 Geometridae (Fox *et al.* 2013).

In concordance with others (Rydell 1992; Kolligs 2000; Eisenbeis 2006; Eisenbeis & Eick 2011; van Langevelde *et al.* 2011; Barghini & De Medeiros 2012), our results indicate that UV/shorter wavelength rich lighting is likely to have a greater impact on moth populations, with potential effects at higher trophic levels (Rydell 1992), and support the advocacy of lighting types lacking such shorter wavelengths in ecologically sensitive situations.

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Figures

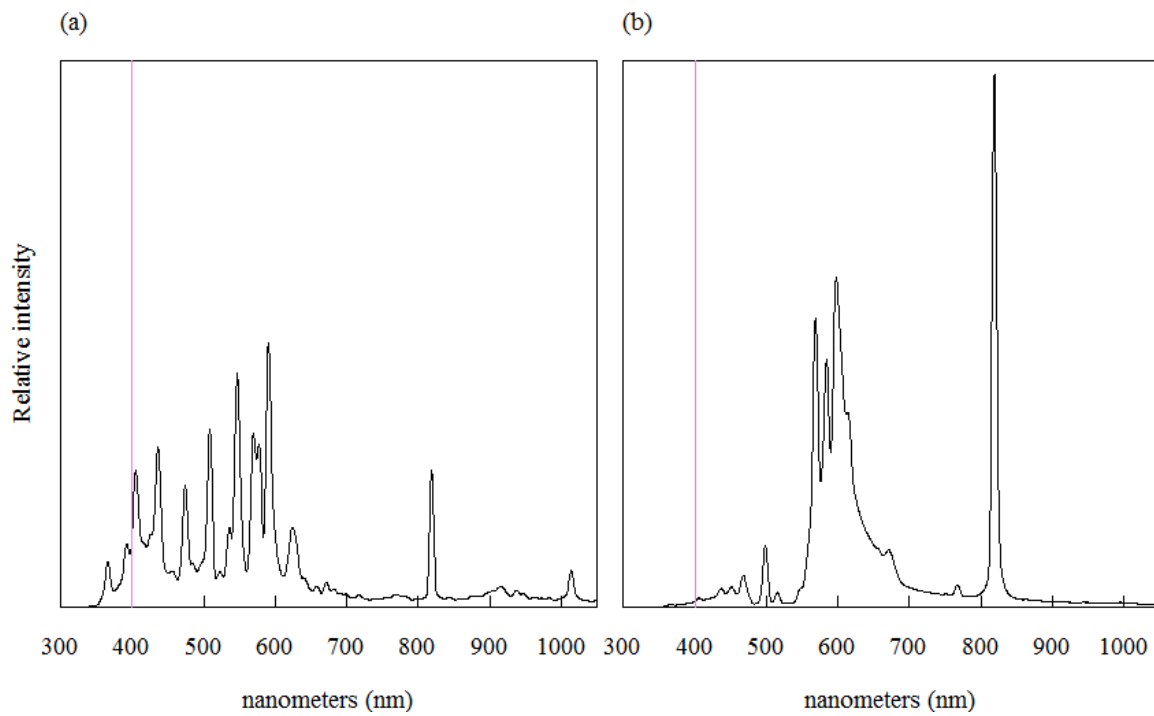


Figure 2.1: Spectral energy distribution of the lights used in the study; (a) shorter wavelength light (weighted-mean wavelength= ~583nm), (b) longer wavelength light (weighted-mean wavelength= ~656nm). Spectra to the left of the violet line is ultraviolet (<400nm). Spectral energy data was measured using an Ocean Optics Maya 2000 spectrometer.

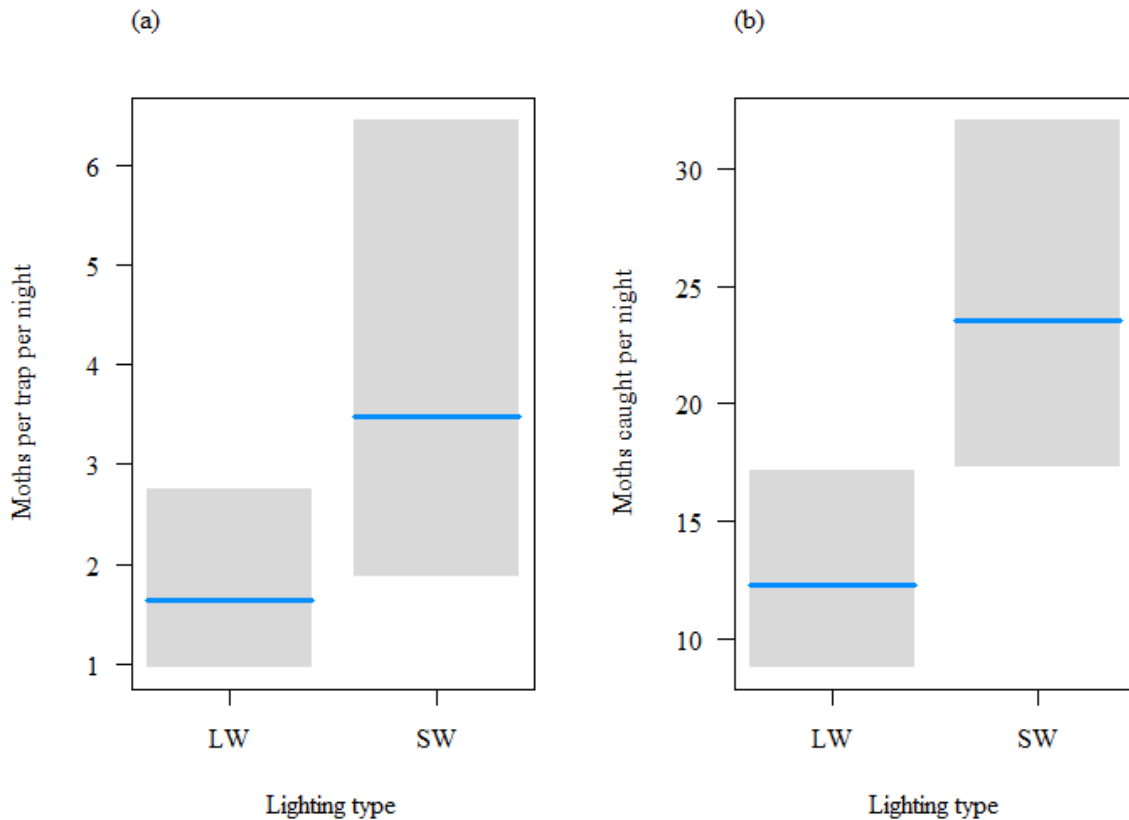


Figure 2.2: (a) Model predictions of the mean number of moths caught per trap per night (blue line) \pm 95% confidence intervals (grey shading) in the two lighting treatments (competitive lighting setup). (b) Model predictions of the mean number of moths caught per night (blue line) \pm 95% confidence intervals (grey shading) in the two lighting treatments (non-competitive lighting setup). LW (longer wavelength), SW (shorter wavelength). Predictions based on data used to fit the model, with environmental covariates set to their median where applicable.

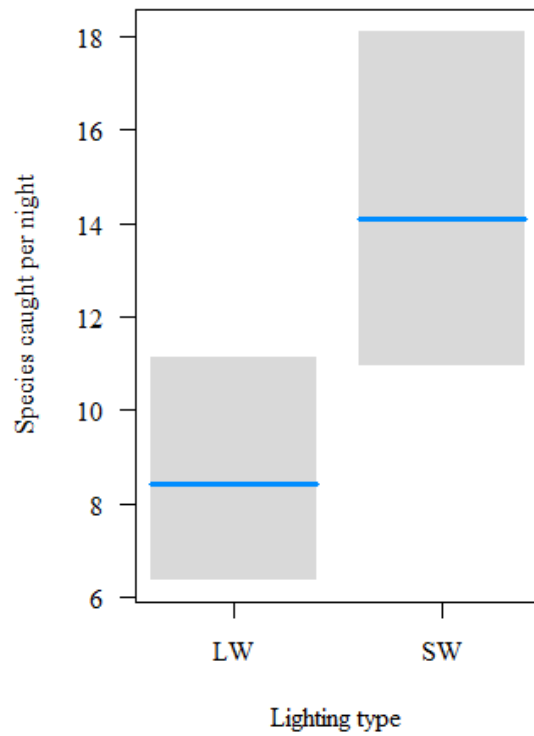


Figure 2.3: (a) Model predictions of the mean number of species caught per night (blue line) \pm 95% confidence intervals (grey shading) in the two lighting treatments (non-competitive lighting setup). Predictions based on data used to fit the model, with environmental covariates set to their median.

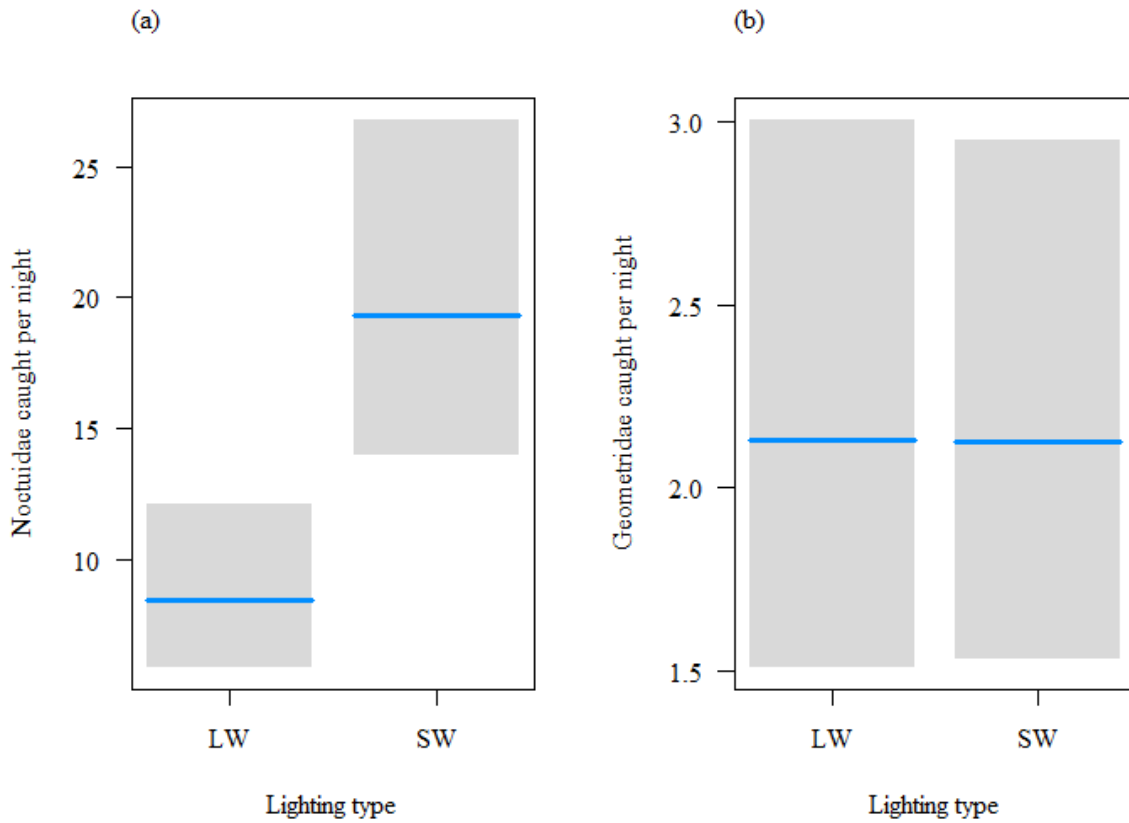


Figure 2.4: Model predictions of the mean number (blue line) of (a) Noctuidae and (b) Geometridae moths caught per night \pm 95% confidence intervals (grey shading) in the two lighting treatments (non-competitive lighting setup). Noctuidae $n=570$, Geometridae $n=81$. Predictions based on data used to fit the model, with environmental covariates set to their median.

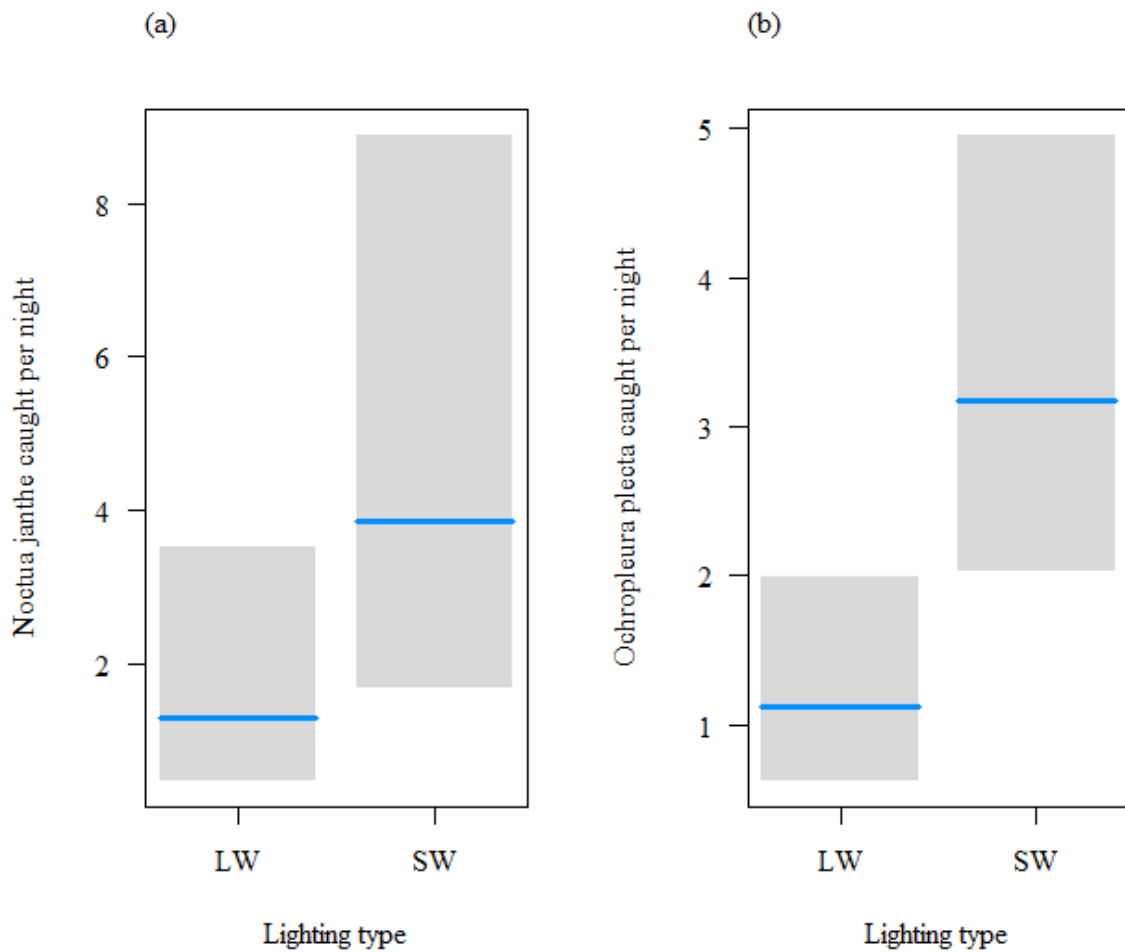


Figure 2.5: Model predictions of the mean number (blue line) of the two most abundant species of moth caught during the experiment per night in the two lighting treatments \pm 95% confidence intervals (grey shading), (non-competitive lighting setup), (a) *Noctua janthe*, (b) *Ochropleura plecta*). *Noctua janthe* $n=118$, *Ochropleura plecta* $n=84$ Predictions based on data used to fit the model, with environmental covariates set to their median.

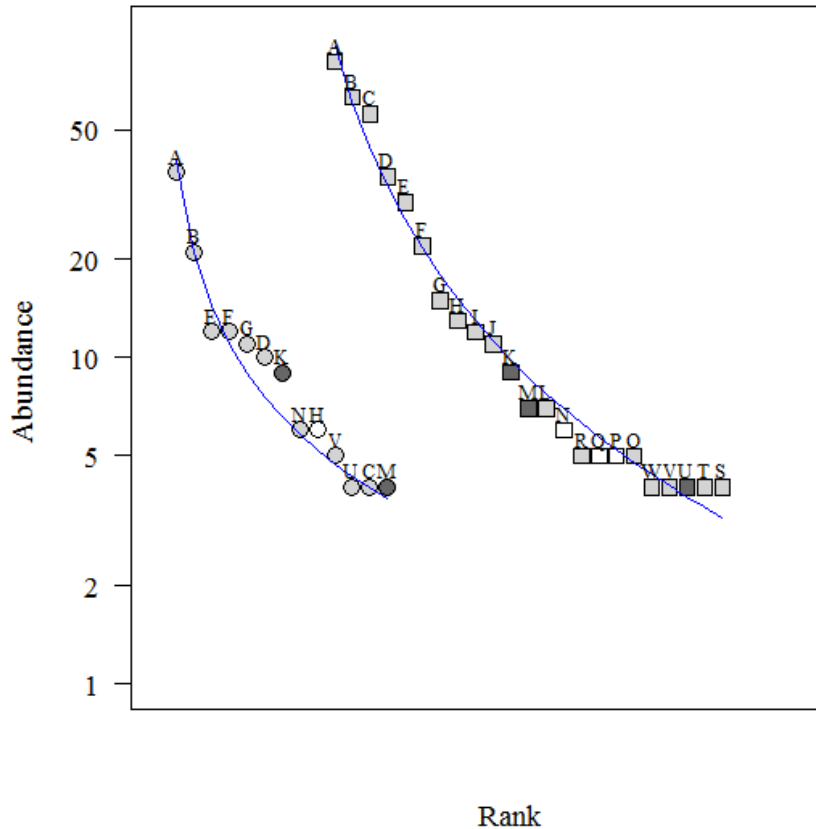


Figure 2.6: Rank abundance curves for lighting treatments where overall moth species abundance is greater than or equal to 4. Longer wavelength (circles) and shorter wavelength (squares). Noctuidae (light grey), Geometridae (white) and other (dark grey). A, *Noctua janthe*; B, *Ochropleura plecta*; C, *Noctua pronuba*; D, *Autographa gamma*; E, *Hoplodrina alsines*; F, *Mesapamea secalis* agg; G, *Xestia c-nigrum*; H, *Phlogophora meticulosa*; I, *Agrostis exclamationis*; J, *Agrostis puta*; K, *Eilema Griseola*; L, *Eilema depressa*; M, *Apamea monoglypha*; N, *Idaea biselata*; O, *Melanchra persicariae*; P, *Idaea aversata*; Q, *Ecliptopera silaceata*; R, *Abrostola tripartite*; S, *Cosmia trapezina*; T, *Noctua comes*; U, *Miltochrista miniata*; V, *Hydraecia micacea*; W, *Rivula sericealis*.

Appendices 2



Figure A2.1: photograph of safari moth trap containing standardised amount of seedling trays, suspended from one of the lamppost structures.



Figure A2.2: lamppost structures mounted on wall, illustrating difference in height between the front and the back.

Supplementary methodology

Moth family classification

Moths caught during the study were classified into families as outlined in “Field Guide to the Moths of Great Britain and Ireland” (Waring et al. 2009)

In situ release of captured moths/removal of individuals for identification

As the moths were released in situ regardless of lamp type, and the removal of certain moths for further identification was deemed effectively random, neither process was thought likely to bias the results one way or another.

References

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Chapter 3: LED lighting and the attraction of moths: do families respond differently?

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Keywords: Metal halide, street lighting, moths, light pollution, insect attraction, urbanisation, ecological impact

Abstract

Recent research has highlighted declines in macro moth numbers in Britain and elsewhere in Europe. Given the well-known ‘flight-to-light’ behaviour of moths, and the negative effects this behaviour can have, the increasing amount of artificial light in the environment is a suspected contributor to this decline. Energy efficient LED lighting is being increasingly used for street lighting, and its use is likely to dominate in the near future (Peters 2011). We therefore compared the attractiveness to moths of LED and another modern street lighting option, ceramic metal halide, in an effort to determine which type of lighting is likely to be more detrimental to moth populations. The LED lighting attracted significantly fewer moths than the ceramic metal halide, and this was deemed likely to be predominantly due to the lack of UV

emitted by the LEDs. LED lighting was the less attractive lighting type, regardless of moth family, although model predictions suggested possible variation in the degree to which moth families were more attracted to the ceramic metal halide lighting; further research would be needed to determine this. LED lighting is likely to be a relatively moth friendly lighting type, and its design flexibility will likely enable the development of even more ecologically friendly street lighting. Further research into the ecological impacts of different colours of LED lighting will help identify universally ecologically sensitive lighting solutions.

Introduction

The relatively recent and rapid proliferation of electric lighting has meant that huge areas of the Earth's surface are now polluted by artificial light (Cinzano *et al.* 2001). Ambient light levels are known to be important to systems that have evolved under natural cycles of light and dark (Hölker *et al.* 2010b) and adverse effects of light pollution on the environment are being increasingly reported (Frank 1988; Longcore & Rich 2004; Navara & Nelson 2007; Hölker *et al.* 2010b; Bruce-white & Shardlow 2011; Davies *et al.* 2012, 2013; Gaston *et al.* 2012; Lyytimäki 2013; van Geffen *et al.* 2014; Perkin *et al.* 2014).

The nocturnal environment is continuing to change, with annual increases in global artificial nighttime light emission estimated to be at about 6% (Hölker *et al.* 2010a). The quality of light in terms of spectra is also changing; driven by advances in technology, the need to reduce energy consumption, and the perceived amenity benefits of certain lighting types. There is an increasing trend for the replacement of longer wavelength, usually yellow or orange, street lighting with shorter wavelength white street lighting, which enables better colour vision for humans (Gaston *et al.* 2012). There are a number of broad spectrum white light sources that are

increasingly being used for municipal street lighting, including high luminosity light emitting diodes (LEDs) and ceramic metal halide lights (Royal Commission on Environmental Pollution 2009). LEDs are being increasingly utilised due to recent technological developments that have enabled the energy efficient production of high luminosity white light (Pimputkar *et al.* 2009) . It has been estimated that the LED market will represent 60% of total global lighting by 2020 (Peters 2011).

Due to the well-known 'flight-to-light' behaviour of moths, and the results of a number of studies exhibiting detrimental consequences of light attraction, such as predation by bats (Rydell 1992; Svensson & Rydell 1998), artificial light pollution is considered a potential contributor to the apparent declines in the numbers of European macro moths (Conrad *et al.* 2006; Mattila *et al.* 2006, 2008; Groenendijk & Ellis 2010; Fox 2012; Fox *et al.* 2013). A number of studies have set out to compare the attractiveness of different types of light to find out which types of lighting are likely to have the least ecological impact (Eisenbeis 2006; Eisenbeis & Eick 2011; van Langevelde *et al.* 2011; Barghini & De Medeiros 2012; Somers-Yeates *et al.* 2013). The results of all the previous studies suggest that shorter wavelength lighting is more attractive to insects as a whole, and that UV light is particularly attractive. However, given that the degree of attraction to different spectra of lighting has been shown to vary between different orders of insects and families of moth (Somers-Yeates *et al.* 2013; van Grunsven *et al.* 2014), it is important to focus on how such families will respond to modern lighting technologies. Despite the projected dominance of LED lighting, to the best of our knowledge, only three published studies have looked at insect attraction to LEDs (Eisenbeis & Eick 2011; Poiani *et al.* 2014; van Grunsven *et al.* 2014), and only one of these previous studies looked specifically at street lights. Here we use an experimental street light setup to make a

comparison of LED lighting with ceramic metal halide lighting, in terms of their attractiveness to UK macro moths.

Materials and methods

Study area and lighting

Experiments were performed in the Walled Garden, Penryn Campus, Penryn, UK (Latitude/Longitude: 50.169457/ -5.1244813). Trapping took place on 32 nights between 21st June 2013 and 10th October 2013. Four lamp-post structures were mounted on a wall overlooking the site. Two adjacent lights were suspended from each lamp-post; a Lumino cool white LED floodlight (70W, 4,250 lm), and a Phillips crisp white Master Colour, ceramic metal halide (MH) floodlight (150W, 14,200 lm) (see figure 3.1 for their spectral properties). These specific floodlights were chosen due to their structural similarity. Lighting type was selected on each lamp-post with a switch. The lamp-posts were positioned approximately 14.5 m apart and the lights were angled at approximately 45°. The lights were ~5.65m above ground level in front of the wall and ~3.1m above the ground level behind the wall; see figure A 3.1 (appendices 3).

On any given night, all of the lamp-posts displayed the same lighting type. The lighting type was alternated on consecutive nights of trapping. Lights were turned on and off automatically by a photocell at dusk and dawn. Macro moths were trapped with safari moth traps suspended below each of the lights; see figure A3.2 (appendices 3). Seedling trays were used within the traps as refuge for the moths. The traps were checked every morning, and moths were collected live and identified to species level where possible. Species identification took place at the site, and

identified individuals were released in situ. If species identification was not possible in situ, samples were taken from the site for further inspection.

Statistical analyses

A generalised linear model with negative binomial error structure was used to test for differences between the two lighting types in nightly pooled moth abundance. Moth abundance was incorporated into the model as the response variable, with lighting type incorporated as the explanatory variable. To account for the influence of environmental conditions on moth abundance, daily averages of temperature (°C), rainfall (mm), wind speed (km/h) and lunar phase (% of moon visible), for the day prior to the morning of moth collection, were incorporated into the model as covariates (weather data was obtained from a weather station at a site ~13km from the study area, via the 'Weather Underground' website <https://www.wunderground.com>). A separate generalised linear model with a negative binomial error structure was used to test whether moth family (categorized as Noctuidae, Geometridae, Other) affected number of moths caught at the two lighting types; again, moth abundance was incorporated into the model as the response variable, with light type, moth family, and their interaction included as fixed effects, and the same aforementioned environmental variables as covariates. The negative binomial error structure was chosen for both the previous models as the count data was found to be overdispersed. The overall species richness of the moths attracted to the two lighting types was compared using a general linear model with a poisson error structure; species richness was incorporated into the model as the response variable, with lighting type as the explanatory variable; the same environmental variables as were previously mentioned were again incorporated into the model as covariates. Tests of significance were carried out with likelihood ratio

tests, comparing into the model as null models with alternative models. Model selection was based on comparative model check plots of residual versus fitted values, and checks of normality of the residuals. The statistical analyses were carried out using R (v. 64 3.0.3) (R Core Team 2014) and glmmADMB (v. 0.7.7) was used for the generalized linear-mixed effects model (Skaug *et al.* 2013).

Results

Over 660 macro moths were caught during the study; 505 Noctuidae, 63 Geometridae and 60 Others (The remaining moths, not classified to the family groups, were macro moths that escaped from the trap during collection, meaning identification to family level was not possible). Significantly more moths were trapped at MH than LED lighting (glm.nb, *Likelihood ratio statistic*₁= 40.6, $p < 0.001$, $n = 32$) (figure 3.2). There was a non-significant interaction between lighting type and moth family (glm.nb, *Likelihood ratio statistic*₂= 4.7, $p = 0.09$, $n = 32$, figure 3.3). Significantly more species were also trapped at MH than LED lighting (glm, $\chi^2_1 = 54.4$, $p < 0.001$, $n = 32$) (figure 3.4).

Discussion

Significantly fewer moths of fewer species were trapped at LED than MH lights during this study. This result agrees with studies by Eisenbeis & Eick (2011) and van Grunsven *et al* (2014). van Grunsven *et al* (2014), using modified Robinson traps at ground level to compare of the attractiveness of similarly intense LED and MH lighting to moths, found very similar results to the present study (van Grunsven *et al.* 2014); ~4.4 times more macro Lepidoptera were attracted to the ceramic metal halide lighting than LED lighting used in their experiment (personal communication).The difference is likely to be predominantly due to the lack of UV

light emitted by LED compared with MH lamps (figure 3.1) (Eisenbeis 2006; Eisenbeis & Eick 2011; van Langevelde *et al.* 2011; Barghini & De Medeiros 2012; Somers-Yeates *et al.* 2013; van Grunsven *et al.* 2014). The addition of a UV filter to a mercury vapour lamp reduced the Lepidoptera catches by ~3.8 fold (Barghini & De Medeiros 2012), not so dissimilar to the ~6 fold difference between LED and MH lights in our study. The difference in the number of moths attracted to the two lamp types in our experiment could also be driven in part by the overall reduced intensity/amount of light emitted by the 70W LED, compared to the 150W MH lamp. However, the intensity of a light source is known to be less important than its spectral composition, in terms of how attractive it is to insects (Longcore *et al.* 2015). In contrast to our previous findings, which showed a lack of phototactic preference by Geometridae for either high pressure sodium or MH lighting but a clear preference for MH lighting amongst Noctuidae (refer to chapter 2 & Somers-Yeates *et al.* 2013), a non-significant interaction between lighting type and moth family in the present analysis would suggest that this is not the case when comparing these two lighting types. Interestingly however, predictions from the full model used to test the aforementioned hypothesis, suggest that the degree to which moths are more attracted to the MH than the LED lighting may differ between moth families; more data would be needed to further explore this. The model predictions suggest a ~seven-fold and ~five-fold difference for Noctuidae and Other families respectively, but only a ~two-fold difference for Geometridae. We were interested in trying to identify any moth family variation in phototactic preference for different lighting types as it could be useful to know if trying to determine the possible contribution artificial lighting has made to the decline in macro-moth numbers in Britain. For example, assuming that increased attraction to light results in increased moth mortality, one

might expect more marked differences in declines of noctuid populations between areas predominated by MH lighting than LED lighting, when compared to geometrid populations; assuming the aforementioned predicted variation between families proved to be significant through further data collection and analysis.

Although the findings of this experiment suggest that this LED lighting is likely to be less attractive than the MH lighting, this does not mean that other LEDs could not be particularly attractive to insects; LEDs are variable. Indeed, some have suggested that LED lighting is likely to worsen ecological light pollution (Pawson & Bader 2014). In addition, white LED street lighting has been shown to have negative impacts on bat flight behaviour, and moth development (Stone *et al.* 2012; van Geffen *et al.* 2014), and may have, as yet undiscovered, ecological impacts. However, the majority of studies which have looked at the attractiveness of LEDs to insects in comparison to other lighting types tend to find LEDs to be less attractive (Eisenbeis & Eick 2011; van Grunsven *et al.* 2014; Longcore *et al.* 2015), and thus LED street lighting is likely to be a good, ecologically sensitive option compared to other modern street lighting types; reducing moth attraction regardless of family. LED lighting is favoured for its design flexibility, and ability to produce different colours of light. It is also controllable and can be incorporated into intelligent and centrally controlled lighting systems, which enable the operational times of the light to be adjusted remotely (Peters 2011; Gaston *et al.* 2012). Therefore, further research into different colours of LED lighting, light intensity, and the time of night during which lighting has its greatest impacts will be useful in highlighting more universally ecologically sensitive lighting solutions. Further understanding of how individual groups of organisms, such as moth families, are impacted by artificial light will be useful for situations where populations of the given taxa are particularly under threat, whereas

studies at a community level will be useful for identifying more universally sensitive lighting solutions.

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Figures

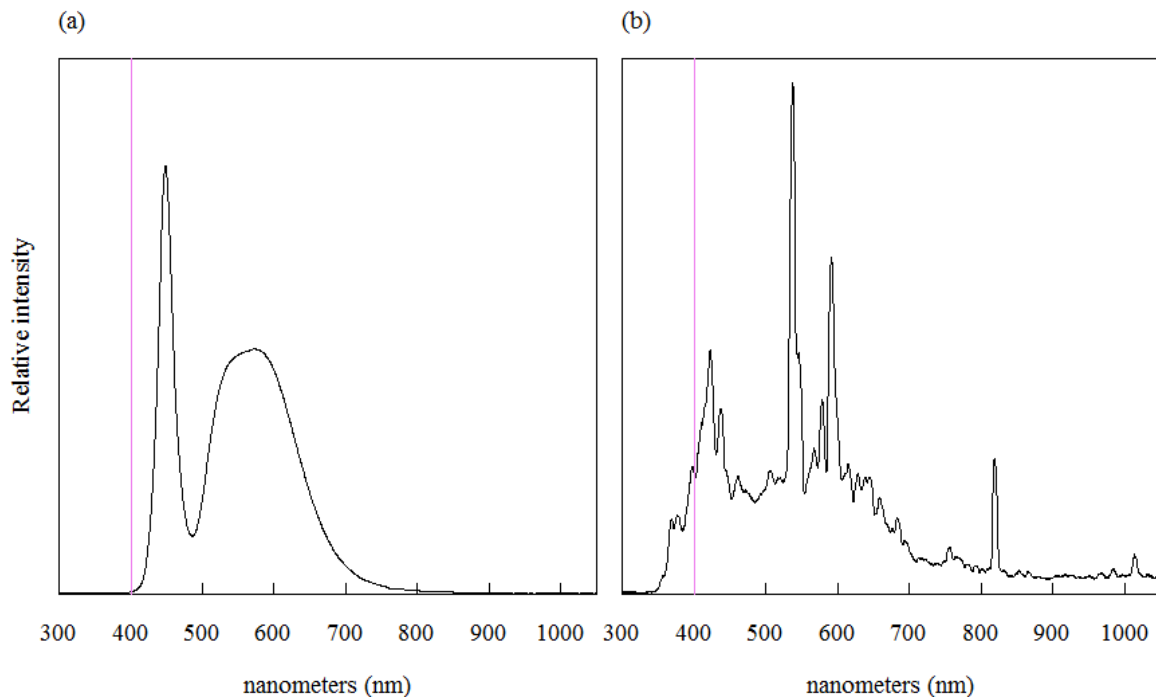


Figure 3.1: Spectral energy distribution of the lighting used for the study (a) = LED (weighted-mean wavelength= ~549nm), (b) = MH (ceramic metal halide) (weighted-mean wavelength= ~580nm). Spectra to the left of the violet line is ultraviolet (<400nm). Spectral energy data were measured using an Ocean Optics Maya 2000 spectrometer.

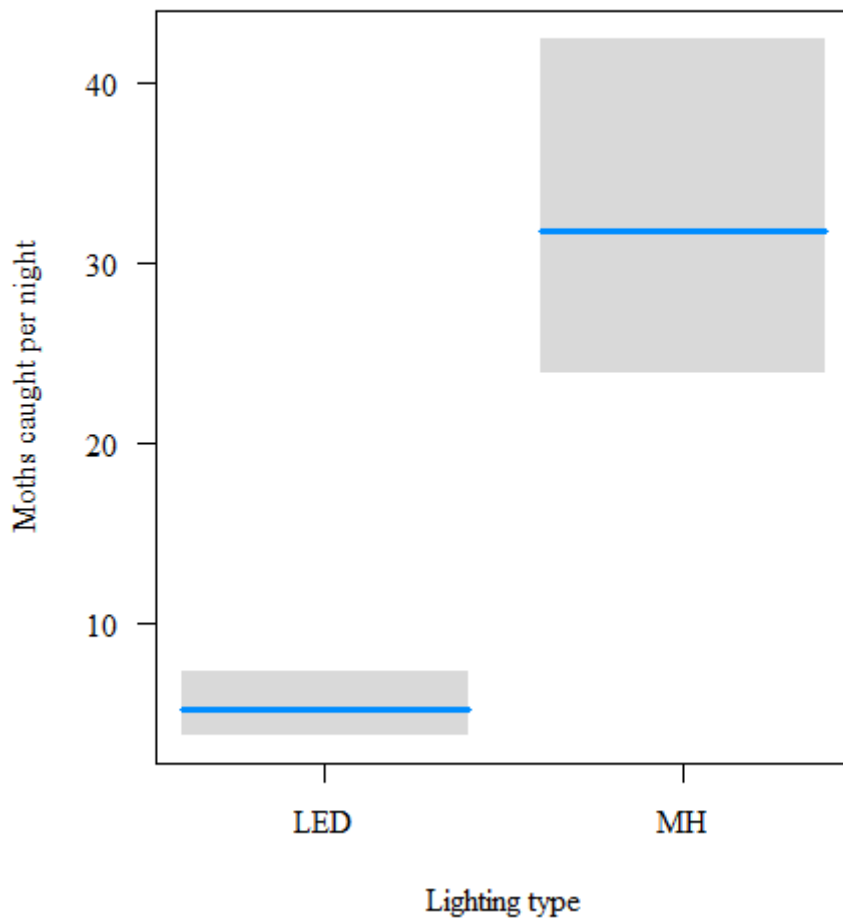


Figure 3.2: Model predictions of mean number of moths caught per night (blue line) \pm 95% confidence intervals (grey shading) in the two lighting treatments, LED and MH (ceramic metal halide), (n= 32 nights). Predictions based on data used to fit the model, with environmental covariates set to their median.

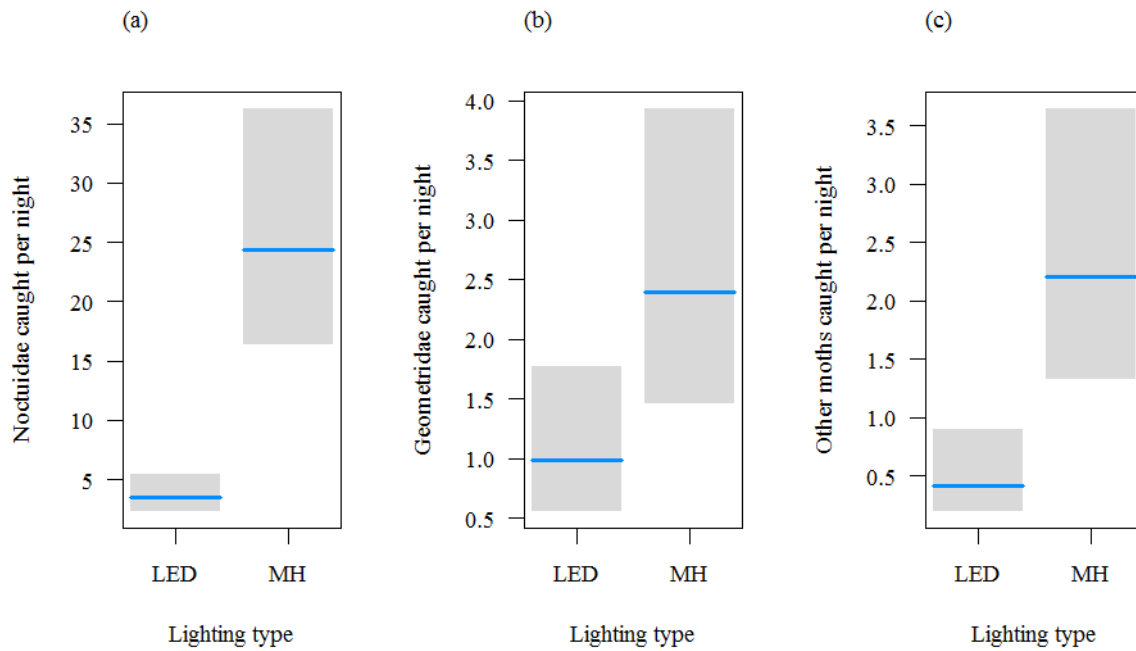


Figure 3.3: Model predictions of mean number of moths caught per night (blue line) \pm 95% confidence intervals (grey shading) in the two lighting treatments, LED and MH (ceramic metal halide), (n= 32 nights). (a) = Noctuidae, (b) Geometridae, (c) macro moths from all other families. Predictions based on data used to fit the model, with environmental covariates set to their median.

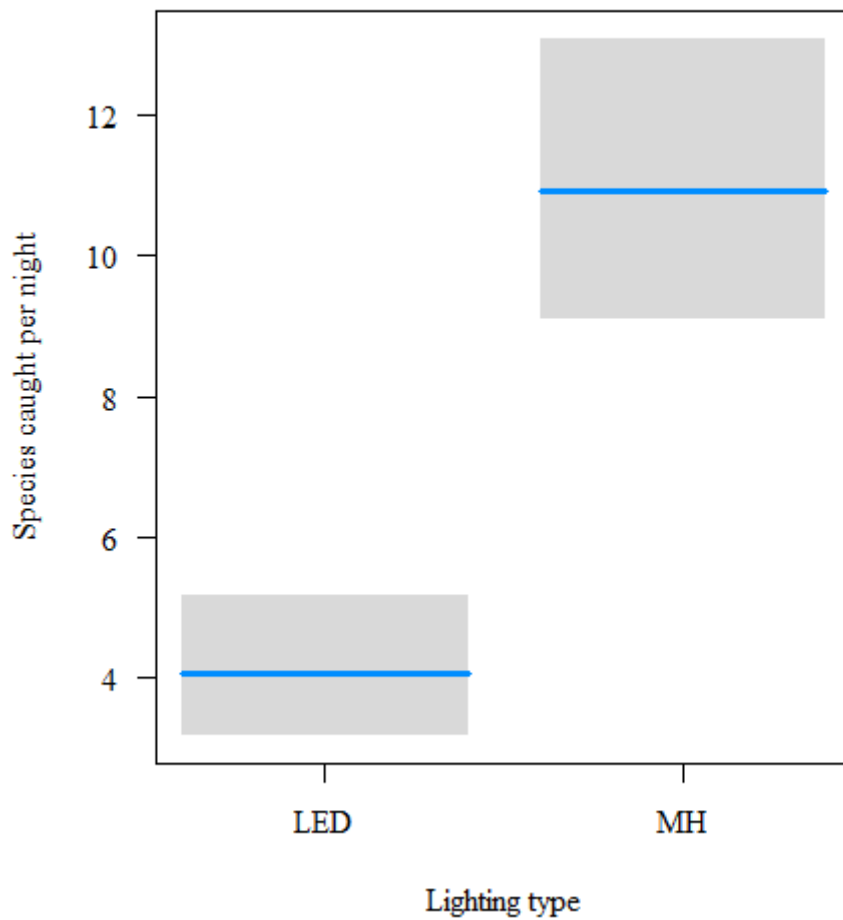


Figure 3.4: Model predictions of mean number of species caught per night (blue line) \pm 95% confidence intervals (grey shading) in the two lighting treatments, LED and MH (ceramic metal halide), (n= 32 nights). Predictions based on data used to fit the model, with environmental covariates set to their median.

Appendices 3



Figure A 3.1: lamppost structures mounted on wall, illustrating difference in height between the front and the back; $5.65\text{m} \pm 0.13$ s.d. above ground level in front of the wall and $3.1\text{m} \pm 0.33$ s.d. above the ground level behind the wall.



Figure A 3.2: Photograph of Safari moth trap suspended below one of the lamppost structures; lamps act as backboard, deflecting moths into the traps. The LED is on the left of the picture and the ceramic metal halide is on the right.

Supplementary methodology

Moth family classification

Moths caught during the study were classified into families as outlined in “Field Guide to the Moths of Great Britain and Ireland” (Waring *et al.* 2009)

In situ release of captured moths/removal of individuals for identification

As the moths were released in situ regardless of lamp type, and the removal of certain moths for further identification was deemed effectively random, neither process was thought likely to bias the results one way or another.

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Chapter 4: Oak (*Quercus robur*) budburst is advanced in areas with more nighttime lighting.

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Key words: artificial nighttime light; light pollution; phenology; species interactions; oak budburst; ecological impact

Abstract

The ecological impacts of artificial nighttime lighting are of current concern due to the increasingly large amount of global nighttime light pollution and known importance of the ambient light level to organisms. Specifically, concern has been expressed about the potential impact of nighttime light on phenology and knock-on effects on species interactions. Artificial light has the potential to alter the day length as perceived by organisms, which, at mid- to high latitudes, is utilised by certain species as an abiotic cue to ensure the coincidence of development with favourable environmental

conditions. In the present study, a UK wide dataset containing 13 years' worth of citizen science collected, spatially referenced oak (*Quercus robur*) budburst dates was analysed. The spatially referenced budburst dates were matched with satellite imagery of nighttime lighting and average spring temperature data, and the relationship between the variables was analysed. Predictions from generalised additive mixed models fit to the data suggest that oak budburst occurs earlier in brighter areas. In addition, the predicted advance of budburst in brighter areas was still apparent when analysing only the data points that fell outside of large urban areas, where the urban heat island effect is likely reduced. The findings suggest that artificial nighttime light may well be causing an advance in oak budburst, and highlight the need for experimental investigation into the impact of artificial nighttime lighting on phenology and species interactions.

Introduction

Most organisms have evolved for millions of years under predictable, cycles of light and dark resulting from the Earth's rotation and orbit. It is therefore unsurprising that the ambient light level plays an important role in natural systems, acting as a resource and an abiotic cue, organising both daily and seasonal patterns in many organisms' activity (Gaston *et al.* 2013). At higher latitudes, changes in day length are an accurate indicator of the progression of the season, and specifically the onset of more favourable spring conditions (Basler & Körner 2012).

Vascular plants are able to utilise phytochrome photoreceptors to effectively determine the day length, and this ability can assist them in timing key phenological events such as bud burst, flowering and bud set, so that they coincide with favourable environmental conditions (Smith 2000; Basler & Körner 2012; Gaston *et al.* 2013). For many organisms the accurate timing of such events is extremely

important, further, in multitrophic systems, the period of optimal conditions is often governed in part by species at the underlying trophic level (Visser & Holleman 2001). This is exemplified well by the oak tree (*Quercus robur*) and winter moth caterpillar (*Operophtera brumata*) system, which has been well studied in the context of the impacts of anthropogenic climate change on phenology (Buse & Good 1996; Buse *et al.* 1999; Visser & Holleman 2001). Oak likely uses temperature and photoperiod as abiotic cues, to unfurl its buds at a time that will maximise the length of the growing season, while reducing the risk of frost damage (Bennie *et al.* 2010; Basler & Körner 2012, 2014; Phillimore *et al.* 2013). In turn, the winter moth is under pressure to match its egg hatch with that of oak budburst; too early and the larvae may face starvation, too late and they will be required to eat less digestible, tannin rich leaves (Feeny 1970; Buse & Good 1996; Visser & Holleman 2001).

Over the last hundred and fifty years or so, the natural nighttime environment has been drastically altered by the proliferation of artificial light. In 2001, almost one fifth of the Earth's land surface was estimated to be above a light level deemed polluted (Cinzano *et al.* 2001), and global artificial light emission has been estimated to be increasing at a rate of about 6% annually (Hölker *et al.* 2010). The increasingly large amount of artificial night lighting, and known importance of light to natural systems have led to concern over the potential ecological impacts of light pollution (Longcore & Rich 2004; Navara & Nelson 2007; Hölker *et al.* 2010; Gaston *et al.* 2012; Davies *et al.* 2013). Specifically, concern has been expressed about the potential of light pollution to disrupt trophic interactions through artificially altering the day length as perceived by living organisms (Longcore & Rich 2004; Davies *et al.* 2012; Gaston *et al.* 2013).

Here we analyse spatiotemporal data on oak budburst and satellite imagery of nighttime lighting, to investigate whether light pollution is correlated with oak budburst date, and thus has the potential to disrupt an important multitrophic system. Spring phenology has been shown to be advanced in urban areas (Imhoff *et al.* 2000; Roetzer & Wittenzeller 2000; White *et al.* 2002; Zhang 2004; Zhang *et al.* 2004; Neil & Wu 2006; Jochner *et al.* 2012) where there is an increased amount of light pollution (Imhoff *et al.* 1997; Sutton 2003), although distinguishing the potential effects of artificial light from those of higher urban temperatures (the urban heat island effect) is challenging. However, Experiments that artificially altered photoperiod showed that budburst in a number of late successional trees was delayed when the photoperiod was shortened (Basler & Körner 2012, 2014). Also, advanced budburst and delayed leaf fall have been observed in trees found in close proximity to artificial lights (Matzke 1936; Bennie *et al.* 2016), which suggests the perception of a longer day by the trees. We therefore hypothesize that oak budburst will be advanced in more light polluted areas.

Materials and methods

Oak bud burst data

Spatially referenced oak budburst data, from the years 1999-2011 collected and submitted by citizen scientists to the UK phenology network (www.naturescalendar.org.uk), was used for the analysis. After data points without spatially corresponding gridded temperature values were removed, 8908 budburst data points remained. Citizen scientists were asked to record 'budburst' as the date when the colour of the new green leaves is just visible between the scales of the swollen or elongated bud; they were advised, if they were having difficulty in deciding

when to record, to wait until the event was occurring in three plants of the same species within close proximity to each other, to record the trendsetters rather than the extraordinary. The potential recorder bias of this data collection protocol was deemed unlikely to be problematic in the present analyses, as there is no apparent reason why the degree of recorder bias should correlate with the amount of artificial nighttime lighting.

Light pollution data

The global data set of annual nighttime satellite images for the years 1999 - 2011, from the Defense Meteorological Satellite Program's Operational Linescan System (DMSP OLS) was used to quantify the amount of artificial light at the locations of the spatially referenced budburst dates. This data is produced and made publicly available by the NOAA National Geophysical Data Centre (Baugh *et al.* 2010) and has previously been used to map the extent of light pollution (Cinzano *et al.* 2001). These satellite images depict a global, cloud free composite of stable nighttime light at approximately 1km resolution, resampled from data at a resolution of approximately 2.7km. Each pixel is represented by a value of between 0 and 63; a value of zero represents areas of relative darkness, whereas brightly lit urban areas usually saturate at a value of 63. Given the coarse resolution of this data, a spatially referenced budburst date within a bright pixel, for example, will not necessarily be located in a bright area; it is just assumed to be more likely to be. This data will be referred to from hereon as either DMSP data or DMSP value.

Calibration of light pollution data

Accurate inter-annual comparisons of the DMSP data are difficult because the data has been collected by multiple satellites with a lack of onboard inter-calibration between the satellites' sensors, and the gain control of their optical sensors is

changed continually to generate consistent imagery of clouds. This means that a specific pixel value in a given year may not represent the same actual level of brightness as a pixel of the same nominal value in another year. In addition, there are inaccuracies with the geolocation of the DMSP data which result in apparent differences in the location of pixels between years; up to 3 pixels (~ 3km) between some years (Bennie *et al.* 2014). In order to compare images between years, the geolocation errors must therefore be rectified and the images intercalibrated. In this study, correction of geolocation errors and intercalibration of images followed the methods described in a previous study (Bennie *et al.* 2014). ****Calibration of the light pollution data was carried out by Jon Bennie.***

Gridded temperature data

Due to the increased amount of artificial light in urban areas, and the fact that urban areas are known to be warmer than surrounding rural areas because of the urban heat island effect (UHI) (Arnfield 2003), it was anticipated that temperature would positively co-vary with the amount of artificial light. In an attempt to control for this potential covariance, 5km x 5km gridded mean monthly air temperature data was incorporated into the analysis. This gridded air temperature data covers the majority of the UK and was created using weather station data, through an interpolation process that takes into account topographic, coastal, and urban features (Perry & Hollis 2005) (www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/). For the present analysis, a new 5km x 5km gridded dataset of average spring air temperatures was created from the monthly gridded temperatures. This was done by averaging the temperatures for the period of February to April. These months were chosen to create the average spring temperatures, as the timing of first leaf date in oak is known to strongly correlate with temperatures within this time window (Sparks

& Carey 1995). For the present analyses we used mean spring temperatures for each year corresponding to the years for which we had oak budburst data (1999-2011).

Spatial matching of datasets

Budburst data points were spatially matched up with both DMSP light pollution values, and mean air temperature values, for the corresponding years of budburst data. This spatial join was done using ArcGIS 10. The budburst data was transformed from British National Grid (BNG) to WGS1984 before extracting the DMSP values (See figure 4.1).

Statistical analyses

A generalised additive mixed model with a scaled t-distribution was used to analyse the relationship between the amount of light pollution and the date of bud burst. Bud burst date, quantified as the number of days from January the 1st in the corresponding year, was incorporated in to the model as the response variable, assumed to follow a t-distribution (a symmetric distribution like the Gaussian but with heavier tails). The mean of the response μ was modelled in terms of additive influences from the various predictors; specifically, smooth nonparametric functions of the DMSP value, mean spring air temperature, and their interaction. Calendar year was incorporated into the model as a random effect to account for inter-annual variation of budburst date. To allow for latitudinal variation in day length and other spatial trends in the data, parametric linear and quadratic terms of Easting, Northing and their interaction were also incorporated additively in the mean of the response. An interaction between DMSP value and temperature was included to analyse whether the relationship between budburst date and DMSP value varied at different temperatures. In an additional attempt to exclude the influence of the UHI, the

analysis was repeated using a subset of the data, excluding data points found within large urban areas; the Ordnance Survey Meridian 2 dataset was used to define the urban area boundaries, and the analysis was carried out on the data points that fell outside of settlements with a population of $\geq 125,000$. Data points from Northern Ireland were also excluded from this analysis as the Ordnance Survey Meridian 2 dataset did not cover this area of the UK. Predictions from these models, within the limits of the experimental data used for model calibration, were carried out to aid inference. Due to a paucity of spatially referenced budburst dates at temperatures of $\leq 3^{\circ}\text{C}$, the analysis of all the data was repeated using only the data points found in areas of $\geq 4^{\circ}\text{C}$ as a means to understand the influence of the outliers on model predictions. The “gam” function from the R package mgcv (v. 1.8-4) was used for fitting the generalised additive mixed models (Wood 2006, 2011), and approximate tests of significance were carried out on the model terms by using the function “anova.gam”; this function carries out Wald tests of significance on the smooth and parametric terms within a single fitted gam object. All statistical analyses were carried out using R (v. 64 3.0.3) (R Core Team 2014). See supporting information for additional information on statistical methods and model check plots.

Results

Oak budburst occurs significantly earlier in brighter areas, with a slightly more pronounced relationship at warmer sites (See figure 4.2, table 4.1; relationship between budburst date and the interaction between the DMSP value and the average spring temperature $\chi^2=880.5$, p (approximate) ≈ 0.001 , $n=8908$). The model predictions suggest that buds of trees in areas that experience average spring temperatures of 3°C are likely to burst ~ 0.8 days earlier, on average, in the brightest areas compared to the darkest areas, whereas the buds that experience average

spring temperatures of 9°C are predicted to burst ~1.9 days earlier, on average, in the brightest areas compared to the darkest. The model fit to the subset of data, excluding data points found within large urban areas, showed a contrasting result to the model fit to the complete dataset; whilst the relationship between budburst date and the interaction between the DMSP value and the average spring temperature was also found to be significant, the direction of the effect was reversed, with a more pronounced relationship between the DMSP value and budburst at cooler temperatures (See figure 4.3, table 4.2; relationship between budburst date and the interaction between the DMSP value and the average spring temperature $\chi^2=31.347$, p (approximate) $\ll 0.001$, $n=5295$). The subset model predictions show that buds of oak trees in areas that experience average spring temperatures of 3°C are likely to burst ~3.8 days earlier, on average, in the brightest areas compared to the darkest areas, and that buds that experience average spring temperatures of 9°C are predicted to burst ~2.7 days earlier, on average, in the brightest areas compared to the darkest; this model suggests a curvilinear relationship between budburst and DMSP value, with most of the advance in budburst date occurring between 0 and ~20 DMSP value, levelling off thereafter. Model predictions from the model fit to a subset of the data, excluding data points found at temperatures of $<4^\circ\text{C}$, were also in contrast to predictions from the model fit to the full data set, although the results do suggest a linear relationship between budburst date and DMSP value, in contrast to the results from the analysis of the data points that fell outside of large urban areas (See figure A4.3, table A4.1 in appendices 4).

Discussion

The results of the present analyses highlight, for the first time at a national scale, a relationship between the amount of artificial nighttime light and the date of oak

budburst; with budburst occurring earlier in more brightly lit areas. The DMSP data has been used previously as a proxy measure of urban extent, as the highest value/brightest DMSP pixels are typically found in large urban areas (Imhoff *et al.* 1997; Sutton 2003), and so these findings are similar to previous findings that found advanced spring time phenology in urban areas (Imhoff *et al.* 2000; Roetzer & Wittenzeller 2000; White *et al.* 2002; Zhang 2004; Zhang *et al.* 2004; Neil & Wu 2006; Jochner *et al.* 2012). However, unlike the previously cited large spatial studies, the present study looked explicitly for the relationship between the amount of nighttime light and oak budburst whilst attempting to account for the temperature increases associated with urban areas. It is possible that the temperature data used in the current study insufficiently represents the UHI. The interpolation process used to create the gridded temperature data utilised an old land use data set from the mid-1970s (Perry & Hollis 2005). In addition, weather stations are necessarily positioned at some distance from buildings, and so urban weather stations used to inform the influence of urban areas in the gridded temperature data may not accurately represent the increased temperatures experienced by trees, which may be situated closer to buildings. This potential under representation of the UHI could mean that the present findings are in actual fact explained by increased temperatures. However, the fact that similar model predictions were obtained from a model fit to budburst data points found outside of large urban areas reinforces the likelihood that it is artificial nighttime lighting causing the advance in budburst as opposed to other potential factors which can vary due to urbanisation, such as temperature, but also humidity, water availability, and chemical pollution levels (Peñuelas *et al.* 2004; Kozlov *et al.* 2007; Honour *et al.* 2009; Jochner *et al.* 2013). The results of all the analyses indicate that the relationship between budburst date and nighttime light

level varies depending on the average spring temperature experienced by trees. However, the model fit to the entire data set contrasts with the two models fit to the subsets of data (data points falling outside of large urban areas & data points found in areas with average spring temperatures of $\geq 4^{\circ}$), in terms of the direction of the interaction; predictions from the model fit to the entire data set indicate that the relationship between budburst date and DMSP value is slightly stronger in areas that experience warmer spring temperatures, whilst predictions from the two models fit to subsets of data suggest a stronger relationship in areas experiencing cooler spring temperatures (figure 4.2, figure 4.3 & figure A4.3). Previous research has illustrated how the effect of photoperiod on the timing budburst can vary at different temperatures (Basler & Körner 2014). A stronger influence of artificial light at night on budburst might be expected in warmer areas, as a reduced effect of photoperiod with increased chilling has previously been described for a number of tree species (Caffarra & Donnelly 2010; Basler & Körner 2014). It has been suggested that photoperiod may substitute chilling effects (Basler & Körner 2014); certain woody plants must accumulate a specific summation of cool temperatures before spring development. Conversely, the slightly stronger relationship between budburst date and nighttime light levels at cooler temperatures, predicted by the models fit to both subsets of data (figure 4.3 & figure A4.2), could also potentially be explained. Budburst of *Picea abies* cuttings taken from higher altitude, colder sites was shown to be more strongly advanced by longer photoperiods than cuttings taken from lower altitude, warmer sites. It is suggested that photoperiod is more likely to influence budburst in trees that have experienced sufficient chilling (Basler & Körner 2012, 2014). Although it is possible to explain both the scenarios predicted by the models individually, it is not so easy to explain the co-occurrence of the contrasting

interactions the different models predict. These contrasting predictions cast some doubt over the validity of the models. It is worth noting however, that such a result may just be difficult to explain; spring phenology is influenced by chilling, photoperiod and temperature, all of which are known to interact in complex, species-specific ways that are as yet to be clearly disentangled (Basler & Körner 2012, 2014).

Whilst the direction of the interaction predicted by the different models is discordant, all the models predict the overall trend for advanced budburst in brighter areas; this result is therefore in less doubt. Many vascular plants contain phytochrome photoreceptors, which, through their response to the red:far red ratio of light, effectively enable such plants to detect day length and thus the progression of the season (Smith 2000; Gaston *et al.* 2013); experiments have revealed how reducing the red: far red ratio of light at dusk and dawn can advance budburst in silver birch (*Betula pendula*) (Linkosalo & Lechowicz 2006), and it is perhaps by this mechanism that artificial light pollution could alter the timing of oak budburst. Interestingly, budburst in the former experiment was advanced by four days when they decreased the red: far red ratio during twilight; this alteration in timing is of a similar magnitude to the advance predicted by the model fit to data points that fall outside large urban areas for trees experiencing 3°C. Although advanced budburst in large tree species has previously been observed within close proximity to artificial lights (Bennie *et al.* 2016), oak is perhaps not the most likely species to be found frequently in brightly lit conditions, such as beneath a street light. Indeed, as previously mentioned, the coarse resolution of the DMSP data means that a spatially referenced oak budburst date located within a bright DMSP pixel will not necessarily be located in a bright area; it is just assumed to be more likely to be. It is perhaps more likely that oak in

brighter areas will be subject to a more low intensity, diffuse increase in ambient light level, through skyglow for example.

Changes in the timing of phenological events, such as oak budburst, have a number of potential implications. While the natural lengthening of days in temperate regions may be a reliable cue for the onset of good growing conditions, artificial increases in day length may provide a misleading signal. Therefore, artificial light could potentially accelerate budburst, exposing buds to detrimental environmental conditions. The potential implications are not only for the species directly affected by the light pollution, but also for dependent species. As previously discussed, the winter moth is under selection pressure to match the timing of its egg hatch with that of oak budburst; early egg hatch can mean starvation for the larvae, and delayed egg hatch can mean the larvae are faced with less nutritious food (Feeny 1970; Buse & Good 1996; Visser & Holleman 2001). In addition, the biotrophic fungal pathogen, oak powdery mildew, caused by the Ascomycete fungus *Erysiphe alphitoides*, is adapted to synchronise its phenology with that of its oak host; asynchrony could have fitness consequences for both pathogen and host (Desprez-Loustau *et al.* 2010). Although the species in these examples have evolved together and thus might be expected to respond to natural environmental cues similarly, this is not necessarily the case for novel stimuli such as light pollution, which up until relatively recently would not have been experienced by these species.

It is uncertain what the effects of artificial light on leaf phenology have on the fitness of individual trees; budburst phenology determines the length of the growing season as well as the exposure of leaf tissue to stresses such as low temperatures, herbivory and pathogens. It may also have implications for other species with trophic links to trees. Light pollution is one of many anthropogenic impacts on the

natural environment that may work synergistically with the detrimental effects of others, and the oak and winter moth system is just one of many biological systems that may be impacted; interestingly, recent research has shown how artificial nighttime light can disrupt the reproductive behaviour of the winter moth (van Geffen *et al.* 2015). Furthermore, if a large woodland species such as oak may be affected by light pollution, smaller plants, which grow on verges and in roadside hedges, below the height of an average street light, are perhaps even more likely to be affected. This is particularly pertinent given that road verges are considered a refuge for many rarer species of plant (Plantlife 2017). The results highlight the need to carry out experimental investigation into the impact of urbanisation, and particularly low intensity, diffuse light pollution, on phenology and species interactions.

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Tables and figures

Table 4.1: Terms and properties of generalised additive mixed model fit to all data.

Response variable	Explanatory terms				Model statistics
<i>Budburst date</i>	Smooth terms	EDF	χ^2	p-value (approximate)	R^2 (adj.)
	ti(DMSP value)	0.0002831	7109.1	<0.001	0.345
	ti(Spring temperature)	2.955	1111.8	<0.001	Deviance explained
	ti(DMSP value, Spring temperature) (interaction)	0.0001536	880.5	<0.001	33.1%
	s(year,bs="re") (random factor)	9.619	598.9	<0.001	REML
	parametric terms	DF	χ^2	p-value	32971
	Northing	1	8.639	0.003	Number of observations
	Easting	1	98.015	<0.001	8908
	Northing:Easting (interaction)	1	58.858	<0.001	
	I(Northing)^2	1	7.090	0.008	
	I(Easting)^2	1	14.099	0.0002	

Table 4.2: Terms and properties of generalised additive mixed model fit to data excluding data points found within large urban areas (population ≥ 125000).

Response variable	Explanatory terms				Model statistics
<i>Budburst date</i>	Smooth terms	EDF	χ^2	p-value (approximate)	R^2 (adj.)
	ti(DMSP value)	2.622	8.727	0.0306	0.36
	ti(Spring temperature)	2.913	578.831	<0.001	Deviance explained
	ti(DMSP value, Spring temperature) (interaction)	0.001	31.347	<0.001	
	s(year,bs="re") (random factor)	9.895	395.440	<0.001	REML
	parametric terms	DF	χ^2	p-value	19683
	Northing	1	7.738	0.0054	Number of observations
	Easting	1	12.818	<0.001	
	Northing:Easting (interaction)	1	39.316	<0.001	
	I(Northing)^2	1	6.234	0.0125	
	I(Easting)^2	1	0.021	0.8848	

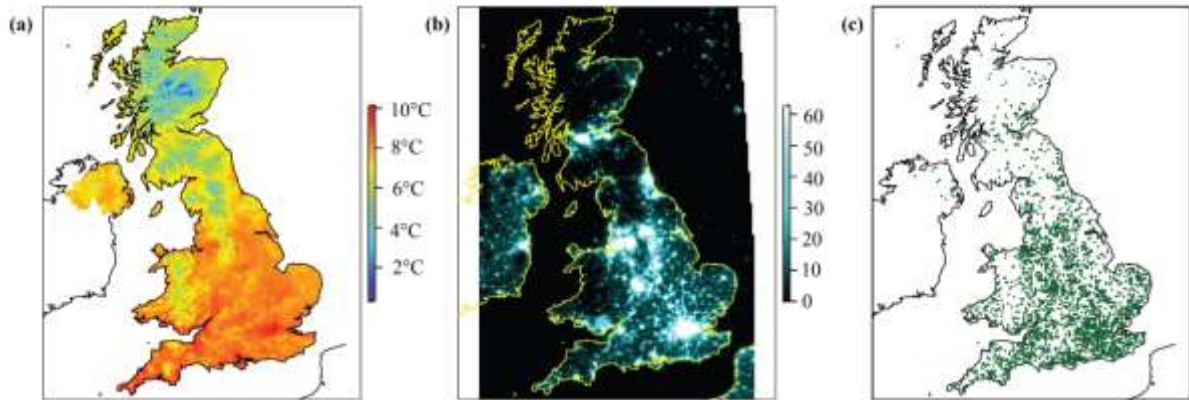


Figure 4.1: Imagery of data used in analysis. (a) Gridded average spring air temperatures in 2011 at 5km x 5km resolution. (b) Nighttime satellite image for the year 2011, from the Defense Meteorological Satellite Program's Operational Linescan System (DMSP OLS), at approximately 1km resolution, resampled from data at a resolution of approximately 2.7km. Each pixel is represented by a value of between 0 and 63; a value of zero represents areas of relative darkness, whereas brightly lit urban areas usually saturate at a value of 63 (refer to Materials and methods for a more detailed description). (c) Locations of oak budburst data for all years.

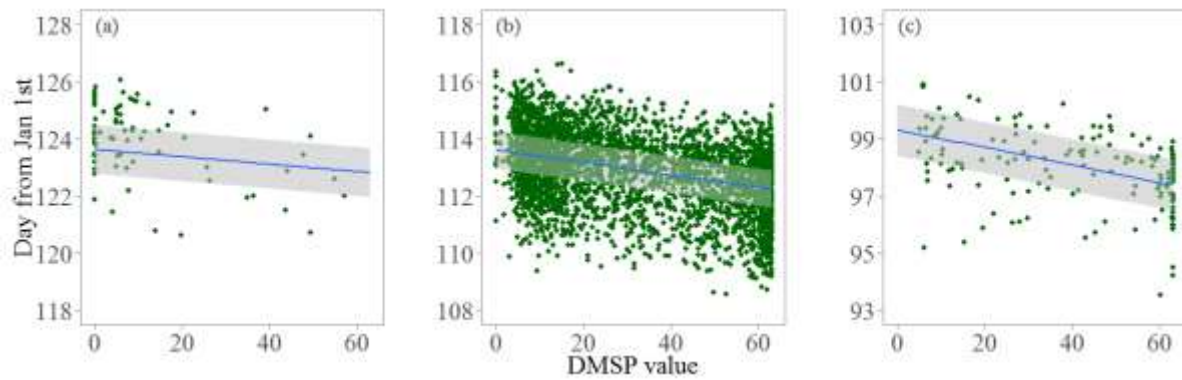


Figure 4.2: Plotted model predictions, within the bounds of the experimental data used for model calibration, of the relationship between DMSP nighttime lights and oak budburst date at different temperatures (a) 3°C, (b) 6°C, and (c) 9°C. Predictions are made for budburst at the mean latitude of data points included in the model. The black line represents the predicted mean and the shaded grey area the predicted 95% confidence intervals. Points represent residuals of individual data points where the spring temperature lies within 0.5°C of the prediction temperature in each panel.

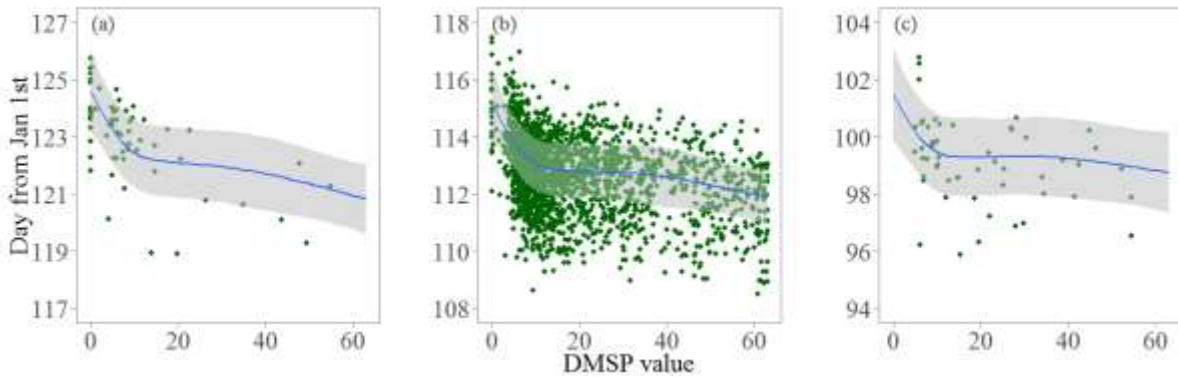


Figure 4.3: Plotted model predictions, within the bounds of the experimental data used for model calibration, from the model calibrated with data points that fall outside of large urban areas (areas with a population of $\geq 125,000$ excluded). Predictions are made of the relationship between DMSP nighttime lights and oak budburst date at different temperatures (a) 3°C, (b) 6°C, and (c) 9°C, and at the mean latitude of data points included in the model. The black line represents the predicted mean and the shaded grey area the predicted 95% confidence intervals. Points represent residuals of individual data points where the spring temperature lies within 0.5°C of the prediction temperature in each panel.

Appendices 4

Notes on model selection

A generalised additive mixed model (gam) from the mgcv package (v. 1.8-4) was chosen to analyse the data as it allowed us to fit a model with a scaled t-distribution (family=scat), which greatly improved model fit in comparison to a Gaussian distribution. Year was incorporated into the model as a random effect using the (... , bs="re") term ("smooth.construct.re.smooth.spec"). The interaction between the DMSP light pollution value and the average spring temperature was included by using tensor product (ti) smooth terms. See (Wood 2011 & Wood *et al.* 2016) for details on the methodology described above.

Tables and figures

Table A4.1: Terms and properties of generalised additive mixed model for all year's data combined. Model based on data excluding data points found at temperatures of < 4°C.

Response variable	Explanatory terms				Model statistics
<i>Budburst date</i>	Smooth terms	EDF	χ^2	p-value (approximate)	R^2 (adj.)
	ti(DMSP value)	0.00001487	69410	<0.001	0.288
	ti(Spring temperature)	0.000009562	1984000	<0.001	Deviance explained
	ti(DMSP value, Spring temperature) (interaction)	0.00004786	1841	<0.001	27.7%
	s(year,bs="re") (random factor)	0.00003905	0.002	<0.001	REML
	parametric terms	DF	χ^2	p- value	32850
	Northing	1	20.22	<0.001	Number of observations
	Easting	1	180.32	<0.001	8811
	Northing:Easting (interaction)	1	58.52	<0.001	
	I(Northing)^2	1	11.48	0.0007	
	I(Easting)^2	1	27.72	<0.001	

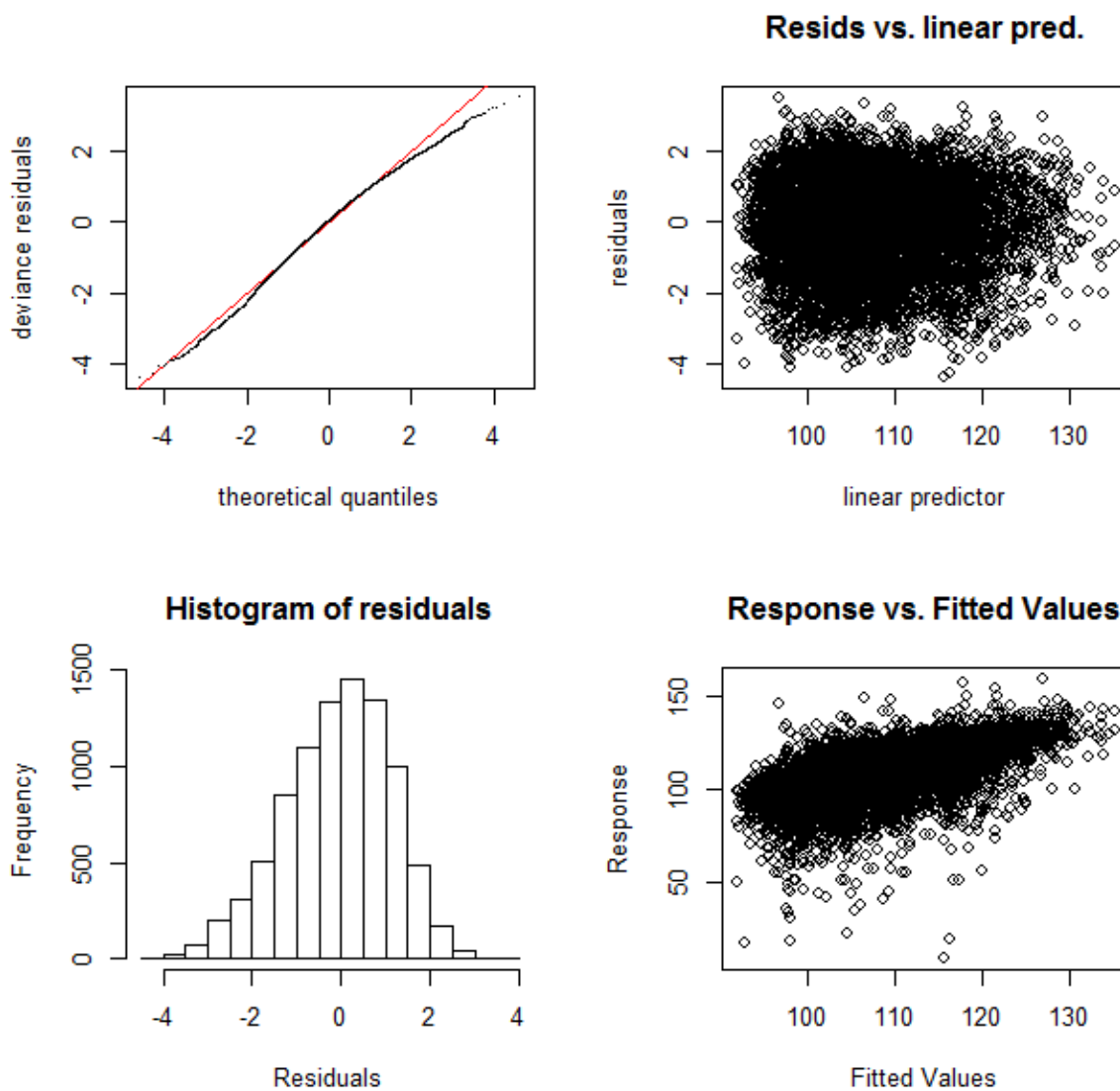


Figure A4.1: Model check plots from model fit to entire dataset. These plots are the default output from the function “gam.check” in the R package “mgcv”. The QQ plot suggests relatively good model fit, and residual vs fitted plot suggests limited, if any, correlation between the residuals and the fitted values. Also there is evidence of strong linear relationship between the actual data and the fitted values (predictions) implying good model fit.

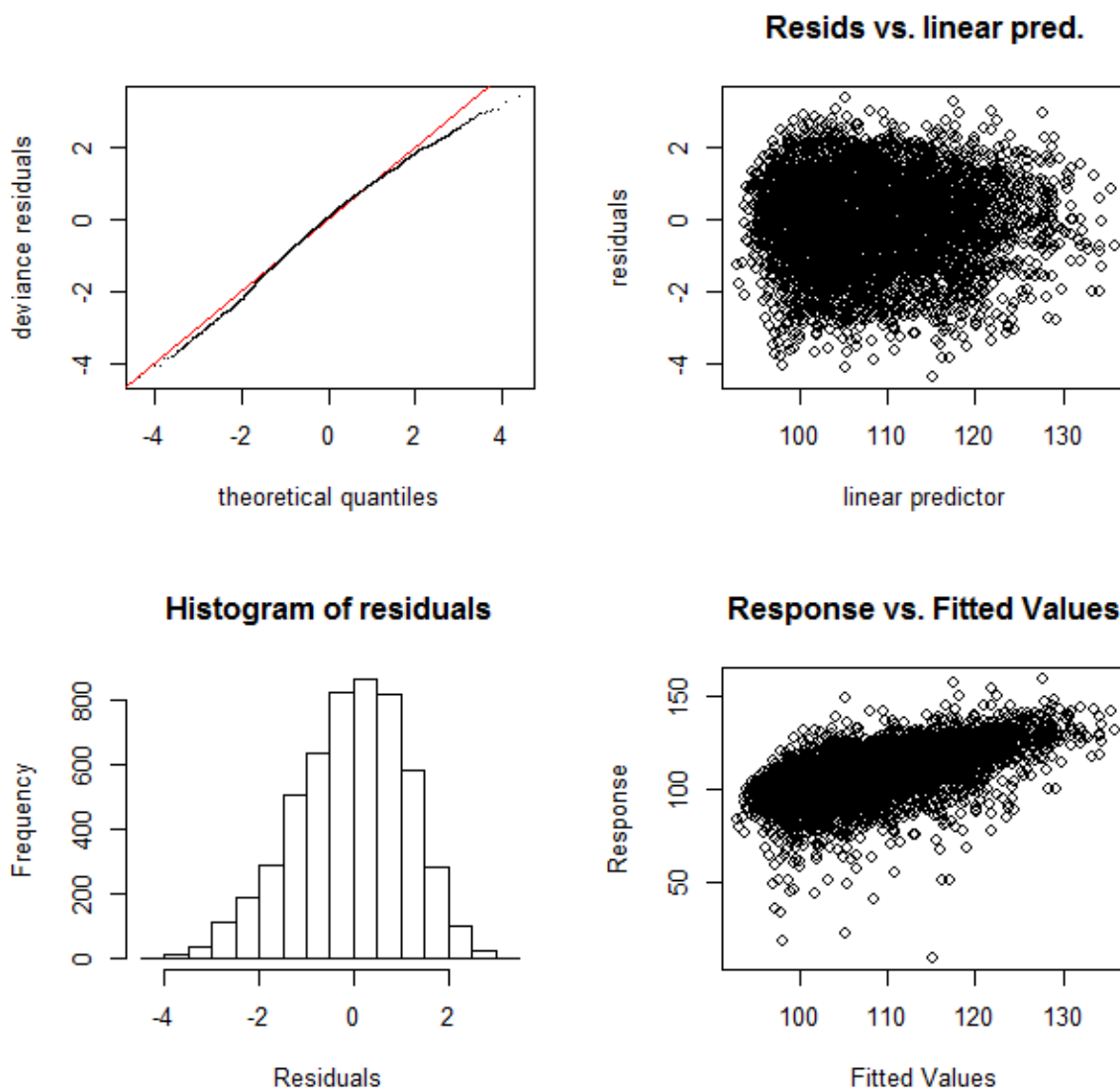


Figure A4.2: Model check plots from model fit to dataset excluding data points from within large urban areas (areas with a population of $\geq 125,000$ excluded). These plots are the default output from the function “gam.check” in the R package “mgcv”. The QQ plot suggests relatively good model fit, and residual vs fitted plot suggests limited, if any, correlation between the residuals and the fitted values. There is also evidence of strong linear relationship between the actual data and the fitted values (predictions) implying good model fit.

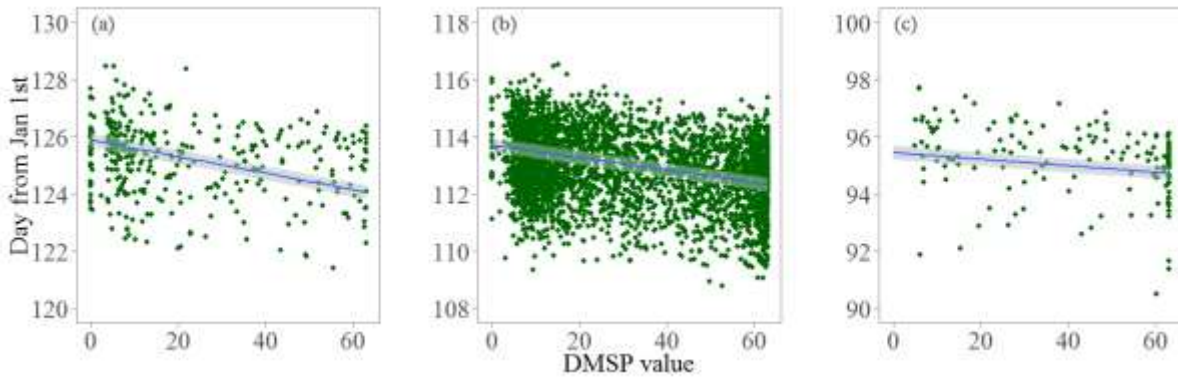


Figure A4.3: Plotted model predictions, within the bounds of the experimental data used for model calibration, of the relationship between DMSP nighttime lights and oak budburst date at different temperatures (a) 4°C, (b) 6°C, and (c) 9°C. The black line represents the predicted mean and the shaded grey area the predicted 95% confidence intervals. Points represent residuals of individual data points where the spring temperature lies within 0.5°C of the prediction temperature in each panel. These plotted model predictions are from the model fit to the subset of data points found in areas of $\geq 4^\circ\text{C}$. Predictions are made for budburst at the mean latitude of data points included in the model. At areas with average spring temperatures of 4°C, buds are predicted to burst ~ 1.8 days earlier in the brightest compared to the darkest areas, as opposed to ~ 0.7 days earlier in areas with average spring temperatures of 9°C. This modelled relationship is qualitatively similar to that of the model fit to the data set excluding points found within large urban areas, and in contrast to that of the model fit to the full data set, with a more pronounced relationship between the DMSP value and budburst date at cooler temperatures. It appears that the relatively few data points found at particularly low temperatures are not having a major influence on the predicted relationship between budburst date and the DMSP value, although the effect size of the relationship between DMSP and budburst date does

seem to be lessened when analysing the data without points found at temperatures of $<4^{\circ}\text{C}$.

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Chapter 5: Investigating some potential effects of low level light pollution on the interaction between winter moth and oak: does artificial light at night affect their phenology?

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Keywords: species interactions; sky glow; artificial light pollution; phenological synchrony; ecological impact; phenology

Abstract

The ecological impacts of artificial nighttime lighting are of concern due to an increasing amount of global nighttime light and known importance of the ambient light level to living systems. Specifically, concern has been expressed about the potential impact of nighttime light on the timing of biological events and, in turn, on species interactions. The winter moth (*Operophtera brumata*) and oak (*Quercus robur*) need to ensure that egg hatch and budburst, respectively, coincide with favourable abiotic conditions. The winter moth also needs to ensure its egg hatch coincides with the oaks budburst, as the caterpillars eat the newly emerged buds. Asynchrony between the phenology of these species could have potentially negative consequences for both species and those at higher trophic levels. This well studied model system was investigated to determine the potential impacts of low intensity

artificial nighttime light on species interactions. Oak saplings and winter moth ova were exposed, from the 19th of December and 30th of January respectively until the end of the experiment, to one of three treatments designed to replicate real world lighting conditions; a yellow light at night treatment, a white light at night treatment and a naturally dark control treatment. In contrast to the findings of Chapter 4, there was no significant relationship found between light treatment and the phenology of either oak budburst or winter moth egg hatch. However, there was a suggestion in the data that the higher buds of the oak saplings emerged earlier in the yellow light treatment. The results are discussed, and further investigation is suggested to better understand the impact of nighttime light on the trophic interaction studied. In addition, further investigation into other biological interactions, perhaps more likely to be subject to heightened levels of artificial nighttime light, is suggested.

Introduction

The nighttime environment has been drastically changed by artificial light over the last 150 years or so. This change has come with the development of electric lighting, and changes in both the amount and type of lighting continue to occur (Hölker *et al.* 2010a; Gaston *et al.* 2012; Bennie *et al.* 2014). Particularly large areas of earth's surface experience artificially heightened light intensities due to both direct illumination by artificial light sources and skyglow, diffuse light pollution scattered in the atmosphere (Kyba *et al.* 2015); in 2001 it was estimated that almost a fifth of the earth's land surface area was above a light level deemed polluted (Cinzano *et al.* 2001). Given the vast amount of artificial light and the known importance of the ambient light level to living organisms it is unsurprising that such artificial nighttime lighting is of concern (Longcore & Rich 2004; Navara & Nelson 2007; Hölker *et al.* 2010b; Gaston *et al.* 2013). Although artificial light has been shown to negatively

impact wildlife in a number of ways , the potential ways in which it could do so are many and largely unknown (Longcore & Rich 2004; Gaston *et al.* 2013).

One potential way in which artificial light can affect natural systems is by artificially altering the day length as perceived by living organisms and thus causing the disruption of trophic interactions (Longcore & Rich 2004; Davies *et al.* 2012; Gaston *et al.* 2013). For many organisms, the ambient light level plays a role as an abiotic cue, organising both daily and seasonal patterns in their activity (Gaston *et al.* 2013). At mid to high latitudes increases in the day length are perceived by many organisms and utilised as a cue to prompt the onset of their development in spring so that it coincides with favourable environmental conditions; for example see (Basler & Körner 2012). The timing of seasonal biological events can be extremely important, and whilst increasing day length is directly related to the conditions favoured by certain organisms, for other organisms the period of favourable conditions is also governed in part by other species at different trophic levels (Buse & Good 1996; Buse *et al.* 1999; Visser & Holleman 2001). This necessary synchrony between one species and another at a different trophic level, and the importance of timing, is illustrated particularly well by the oak tree (*Quercus robur*) and the winter moth (*Operophtera brumata*). Oak is under pressure to ensure its budburst occurs at a time that maximises the length of the growing season whilst minimising the risk of frost damage (Bennie *et al.* 2010). Similarly, the winter moth needs to ensure its egg hatch coincides with favourable abiotic conditions, but also that its egg hatch coincides with the oaks budburst. Winter moth caterpillars eat newly emerged oak leaves; if the eggs hatch before the oak buds burst then the larvae will face starvation, whilst if they hatch too late they will be faced with more mature oak leaves which are tannin rich and less digestible (Feeny 1970; Buse & Good 1996;

Visser & Holleman 2001). Oak and the winter moth have evolved together and as such might be expected to respond to natural environmental cues similarly, however, this is not necessarily the case for novel artificial stimuli such as nighttime light, which up until relatively recently would not have been experienced by either species. Further, what evidence there is suggests that the winter moth may use different environmental cues to oak as a means to achieve synchrony between its egg hatch and oaks budburst, meaning the artificial alteration of one such cue could well disrupt their synchronous relationship; oak likely uses photoperiod and temperature as cues to accurately time its budburst (Basler & Körner 2012, 2014; Phillimore *et al.* 2013), while the winter moth is thought to only use temperature (Salis *et al.* 2016). Disruption to such a system can have knock-on effects at higher trophic levels, for instance, winter moth caterpillars are a known food source for great and blue tits (Buse *et al.* 1999).

Although oak woodland is not the most likely habitat to experience direct, high intensity light exposure, from directly beneath a street light for example, it may well be commonly exposed to low intensity light pollution through skyglow, which has both known and hypothesized detrimental impacts on natural systems despite its relatively low intensity (Moore *et al.* 2001; Kyba & Hölker 2013). In addition, the oak and winter moth make an ideal model system upon which to study the effects of light pollution, and may highlight potential ways in which such light pollution could affect other species, many of which may require synchronous relationships with species at other trophic levels, and generally face increased exposure to light pollution. In this study the effects of various types of artificial light, with different spectral properties, on the timing of oak budburst and winter moth egg hatch are investigated experimentally. Given that longer photoperiods likely advance budburst in oak, and

are not thought to influence egg hatch timing in the winter moth, it was hypothesised that artificial light at night would increase the day length as perceived by oak and thus advance budburst whilst having no effect on the timing of winter moth egg hatch.

Methods

Experimental setup

To create experimental conditions, 18 wooden framed light cages were built and situated within a fenced off compound at the University of Exeter, Penryn campus. Each cage measured 40 x 40 x 60cm (Width x Length x Height), and was covered in anti-thrip netting to reduce the impact of wind and other external environmental factors. The cages were situated in a block with 3 rows of 6 cages; each cage was separated by ~ 1m. The 18 cages were randomly assigned to one of 3 light treatments (white, amber or no artificial light at night (dark control)), resulting in $n = 6$ cages per treatment. Strips of downward facing LED lighting were attached to a central crossbar at the top of the light treatment cages. The white light treatment cages were fit with only 1 cool white LED whereas the amber light treatment cages were fit with a strip of 15 amber LEDs; this was done due to the increased intensity (lux) of the white LED, as a means to more closely match the intensity of the two light treatments (see Figure 5.1 for spectral properties of the light treatments). A photocell was used to automatically switch the light treatments on and off nightly during the experimental period at dusk and dawn respectively. Baffles were attached to the central crossbars of the cages, and opaque fabric to two of the outer sides of the cages to reduce light spill into neighbouring cages (Figure 5.2). The light intensities (lux) of the two light treatment cages varied depending on the height up

the cage measurements were taken. Measurements at the bottom of the cages, at the height of the petri dishes containing the winter moth ova, were on average $\sim 3.6 \pm 0.3$ lux in the white LED cages and $\sim 5.3 \pm 0.6$ lux in the amber LED cages, compared to measurements at the top of the cages, approximately 2 inches directly below the light source, of $\sim 85.4 \pm 22.1$ lux and 67.25 ± 5.6 lux respectively. The dark control treatment measured $\sim 0.015 \pm 0.0016$ lux; measurements were only made at the bottom of the cage in the dark control. All measurements were made in the field on the night of the 3/4/2014, under an overcast sky with no visible moon or stars. 16 of the cages were fitted with iButton temperature loggers for the entire experimental period so as to account for any potential differences in temperature between the cages.

Oak saplings

54 Oak (*Quercus robur*) saplings were obtained from Moor Trees nursery in South Devon, UK. The saplings had been grown from acorns collected throughout Devon; their genetic diversity was unknown, as was the exact age of the saplings, but they were estimated to be no more than 3 years old, and saplings of similar size were selected for the experiment. Saplings were planted in pots measuring $\sim 40 \times 40$ cm within 21 litres of compost (20:1 John Innes No.1 and vermiculite mix). The saplings were collected from Moor Trees nursery on the 3/12/2013, and were potted on the 6/12/2013. Three saplings were planted within each of 18 pots, upon which the light cages described above were securely attached (Figure 5.2). The light cages were switched on, and the oaks subject to the experimental conditions on the 19/12/2013, 2 days before the vernal equinox. Casual surveys of the saplings were carried out regularly until the bud scales were observed to crack, at which point systematic budburst surveys began; the number of burst buds was counted daily where

possible, and buds were deemed burst when the green leaf tip began to protrude from the bud (Figure 5.3).

Winter moth (Operophtera brumata) ova

Winter moth ova, from wild caught females, were obtained from the Netherlands due to a failure to catch any females in the UK. Ten clutches of ova were obtained, each laid by a separate individual parent. The ova were stored in petri-dishes, and kept outside under natural conditions in the Netherlands from the day they were laid up until the day they were posted to the UK on the 28/1/2014. Upon their arrival in the UK on the 30/1/2014, the ova were reintroduced to natural, outside conditions. Prior to the introduction of the ova into experimental conditions, each clutch of ova was divided evenly by 3, and then each sub-clutch was placed on a sheet of filter paper within a separate lidded petri-dish; four holes were drilled into the side of each petri-dish as a means to ventilate the ova and reduce the chance of their desiccation. The petri-dishes were then divided between the light cages, so that ova from each parent were equally present within all 3 experimental treatments. The petri dishes were placed at the base of the light cages on a small block of wood which raised them ~4 inches above the surface of the soil in which the oak trees were planted; this raised position reduced the risk of water inundating the petri-dishes. Due to the fact that there were 30 sub-clutches/petri-dishes of ova, and only 18 light cages, 12 of the light cages contained 2 petri-dishes. The ova were all introduced into experimental conditions on the 4/2/2014, and casual visual surveys were carried out regularly from this date onwards to spot the first signs of hatching. Winter moth ova start out a green colour, and then change to orange before finally darkening prior to hatching; upon arrival in the UK the ova were orange. When casual visual surveys picked up the darkening of the ova, systematic ova counts began. Ova counts were carried out

from digital photographs which were taken daily where possible from directly above the petri-dishes (lids removed for photograph) using an Olympus epm-2 camera with a 14-42mm lens; the photographs were displayed on a computer screen before counts were made. Hatched ova were difficult to see, and the caterpillars could potentially escape through the ventilation holes in the petri-dishes, so apparent disappearance of ova was used as a proxy for egg hatch.

Statistical analysis

To investigate the impact of the light treatments on the date of oak budburst and winter moth egg hatch, the relationship between the date when 50% of buds had burst, and ova had hatched, and the different treatments was analysed. Due to the fact that it was not always possible to count the ova and buds on a daily basis, it was necessary to first interpolate missing counts as a means to calculate the date of 50% budburst and egg hatch for each individual sapling and sub-clutch of ova respectively. To calculate these dates, a generalised linear model with a binomial error structure was used, where for each sapling and sub-clutch of ova, the proportion of buds burst or eggs hatched (binomial response variable) was modelled as a linear function of time (Julian day(explanatory variable)). These models were fit to data ranging between the last date on which no buds had burst or eggs hatched and the first day on which all buds had burst or ova hatched, as revealed by the systematic counts. For some of the saplings and sub clutches of ova, the systematic counts began too late, after budburst and egg hatch had already begun; in these instances the models were fit to all the data collected up until the first day on which systematic counts revealed that all buds had burst or ova hatched. The “dose.p” function from the R package MASS was then used to extract the interpolated date of 50% egg hatch and bud burst. Due to the fact that the oak saplings experienced

higher light intensities at the top of the cages than the bottoms, the process described above was carried out separately on both the high and low oak buds; the higher buds were those found at $> \sim 8$ inches above the soil surface as measured with a wooden frame quadrat, and the lower buds were those found at $\leq \sim 8$ inches above the soil surface. This resulted in two dates of 50% budburst for those saplings which had both low and high buds, and was done as a means to test whether those buds experiencing higher light intensities were more responsive to the different treatments than those experiencing lower light intensities. Once calculated, the dates of 50% budburst and 50% egg hatch were both analysed separately in relation to the different treatments with general linear mixed models.

For oak, the date of 50% budburst for each sapling was incorporated into the model as the response variable, treatment, and its interaction with the height of the buds from which the 50% budburst date was calculated (low or high) as fixed explanatory variables, and both tree identity (ID) and cage ID as random effects. The random effects were included to account for the non-independence of saplings within a single light cage and the repeated measures from individual saplings. Similarly for the winter moth ova, the date when 50% of ova within each sub clutch had hatched was included as the response variable in the model, with explanatory variables of treatment, lay date of the ova, and their interaction; parent and cage ID were included as random effects. The entire process described above was repeated for oak saplings and winter moth ova within the 16 cages that contained iButton temperature loggers, using the number of degree-days as a surrogate for the day of the year; daily degree-days were calculated for each cage by cumulatively summing the daily mean temperatures ($^{\circ}\text{C}$) recorded within each cage, for the period between January 1st until sampling was complete, using 0°C as a base temperature for

degree-day accumulation, as suggested by (Heide 1993). Due to inclement weather during the experimental period, cages were blown over and as a consequence the lights stopped working in some cages on a few occasions. Regular checks meant that lights went for no more than 2 nights without working on these occasions, except for one occasion where 3 cages malfunctioned, and potentially weren't working for 11 nights; the analyses of the data previously described were repeated, excluding data from within these 3 cages.

The proportions of buds burst and ova hatched used in the previously described analyses were calculated as the proportion of the total number of buds or ova deemed viable. For the buds, the total number viable was calculated by counting the number of buds which successfully burst by the end of the experimental period.

During the experiment some buds looked as if they may go on to burst, but before the end of the experiment any further signs of development ceased. Similarly with the ova, some appeared to become mouldy and consequently disappeared, and were thus deemed non-viable, whilst others seemed to cease development; for the latter situations, if, once egg hatch had begun within a sub clutch of ova, hatching or change in ova colour ceased for a period of two weeks, the eggs were deemed non-viable. As a test of whether the treatments had any influence on the viability of buds, a separate analysis was carried out to see whether the number of viable buds was related to the treatment. This was done using a generalised linear mixed model with a negative binomial error structure; the negative binomial error structure was used due to overdispersion in the count data. The total number of viable buds per cage was incorporated as the response variable and treatment as the explanatory variable. The weights (to the nearest 5g) of the saplings immediately prior to potting were incorporated in the model as an offset to account for any differences in sapling

size between the treatments; the number of buds on a sapling was thought likely to be proportional to the size of the sapling. The cage ID was included in the model as a random effect. This analysis was deemed the best possible test of whether the treatment was affecting bud viability, given that the number of non-viable buds could not be calculated as buds were not always visible prior to their development and budburst. The exact number of ova in each sub clutch was known at the beginning of the experiment however, so an analysis comparing the number of non-viable ova between treatments was possible; this was done using a generalised linear model with a negative binomial error structure due to overdispersion of the data. The mean number of non-viable ova per sub-clutch per cage was modelled as the response variable with treatment as the explanatory variable; the number of ova per sub-clutch was averaged per cage due to the fact an equivalent mixed model failed to converge.

For all analyses model simplification was performed, using likelihood ratio tests to determine significance of terms, and all statistical analyses were carried out using R (v. 64 3.0.3) (R Core Team 2014).

Results

Results from ova analyses

There was a non-significant relationship between the date when 50% of ova hatched and the interaction between treatment and lay date; the same was the case for both treatment and lay date as individual terms (Day of 50% hatch analysis: interaction between treatment and lay date; $\chi^2_2=1.2651$, $p=0.5$. Treatment; $\chi^2_2= 0.6944$, $p=0.7$. Lay date; $\chi^2_1= 1.3502$, $p=0.3$, $n= 30$ sub-clutches of ova in 18 cages) (see Figure 5.4 (a)). The results were qualitatively the same for the accumulated degree day

analysis (Degree day analysis: interaction between treatment and lay date; $\chi^2_2=5.4097$, $p=0.07$. Treatment; $\chi^2_2= 0.1467$, $p=0.9$. Lay date; $\chi^2_1= 1.542$, $p=0.2$, $n= 27$ sub-clutches of ova in 16 cages) (see Figure 5.4 (b)), and also for the date analysis of the subset of data from the cages that did not malfunction due to being blown over (Day of 50% hatch analysis: interaction between treatment and lay date; $\chi^2_2=0.5043$, $p=0.8$. Treatment; $\chi^2_2= 1.4806$, $p=0.5$. Lay date; $\chi^2_1= 1.5517$, $p=0.2$, $n= 24$ sub-clutches of ova in 15 cages) (see Figure 5.5). The relationship between the mean number of non-viable eggs per sub-clutch per cage and treatment was not significant ($\chi^2_2= 0.03031717$, $p=0.99$, $n= 18$ cages).

Results from budburst analyses

Likelihood ratio tests suggested that the relationship between the date of 50% budburst and light treatment was not significant regardless of the height of the buds from which the 50% budburst date was calculated (interaction between height up cage: treatment $\chi^2_2= 3.6443$, $p=0.16$; treatment $\chi^2_2= 0.0588$, $p=0.97$, $n= 42$ saplings with viable buds in 18 cages) (see Figure 5.6). The results were qualitatively the same when analysing the relationship between the accumulated degree days at budburst and treatment (interaction between height up cage: treatment $\chi^2_2= 5.398$, $p=0.07$; treatment $\chi^2_2= 0.0702$, $p=0.97$, $n= 39$ saplings with viable buds in 16 cages) (See Figure 5.7). Similar results were also found when analysing only the buds found on saplings within the cages that weren't caused to malfunction by inclement weather; again both treatment and its interaction with the height of the buds from which the dates of 50% budburst were calculated were found to be non-significant (interaction between height up cage: treatment $\chi^2_2= 3.554$, $p=0.17$; treatment $\chi^2_2= 0.2535$, $p=0.9$, $n= 34$ saplings with viable buds in 15 cages) (see Figure 5.8). There

was a non-significant relationship between the number of viable buds per sapling and treatment ($\chi^2_2 = 2.8851$, $p=0.2$, $n= 54$ saplings with viable buds in 18 cages).

Discussion

The results of the present experiment suggest that neither of the light treatments used to mimic potentially real world light pollution scenarios had a significant effect on the timing of oak budburst or winter moth egg hatch. The result for the egg hatch is perhaps to be expected; what little evidence there is suggests that winter moth egg hatch is non responsive to variation in photoperiod (Salis *et al.* 2016). However, the result is not what was hypothesised with regards to the oak; other studies have suggested photoperiodic influence on oak budburst (Basler & Körner 2012, 2014; Phillimore *et al.* 2013). The oak budburst results also fail to give support to light being the causative factor behind the spatial correlation between the amount of artificial light and the timing of *Quercus robur* budburst which was apparent in a previous analysis carried out in part by the present author (Ffrench-Constant *et al.* 2016) (see chapter 4). However, given the variable nature of light and timing within biological systems there are a number of potential reasons for the present result, and its contrast to other findings.

The spectra of artificial light sources used for nighttime lighting can vary greatly, and the spectra of light is known to be an important factor governing its utility by plants (Gaston *et al.* 2013). Although the white LED treatment used in the current experiment is relatively broad spectrum, it emits limited, if any, UV or far red light, which are both spectra of light known to be utilised by living organisms for various purposes. In plants, the ratio of red to far red ratio of light is known to play a role in their effective perception of day length. Experimental reduction in the red: far red ratio of light at dusk and dawn was shown to advance budburst in silver birch (*Betula*

pendula) (Linkosalo & Lechowicz 2006). Based on the reasoning in the aforementioned experiment, and given the limited far red light emissions of the two light sources used in the present experiment, alongside the red light emissions in the case of the white LED, a lack of advance in budburst is perhaps unsurprising. Indeed, although not apparent in the current results, a delay in budburst might be expected due to the potentially increased ratio of red: far red light caused by red light emissions from the white LED's, if one assumes oak responds similarly to silver birch. The contrast between the findings of this experiment and the suggestion of a relationship between artificial light and earlier budburst, highlighted in chapter 4 and (Ffrench-Constant *et al.* 2016), could be due to a difference between the lighting used in the experiment and the average lighting experienced by real world trees. It could also be due to the fact that immature saplings were used for the present experiment. Immature seedlings are known to unfurl their buds before mature trees, likely as means gather more light for development prior to the emergence of the overshadowing canopy, and there is also some evidence to suggest that immature trees may utilise environmental cues in a different way to their mature conspecifics (Vitasse 2013). Other experiments which have found photoperiod to influence the timing of oak budburst have used cuttings from mature trees (Basler & Körner 2012, 2014). Alternatively, the lack of response in budburst phenology to the light treatments in the present experiment could simply be due to the fact the sample size wasn't big enough to pick up a signal in a system that exhibits such natural variation, particularly given that the sample size was reduced through disruption of the experiment by inclement weather. The timing of oak budburst can vary between individual trees by approximately 3 weeks (Crawley & Akhteruzzaman 1988);

estimated dates of 50% budburst within the control treatment of the present study varied by more than 4 weeks.

Having discussed the lack of a statistically significant relationship between budburst and the light treatments, it is worth noting that the relationship between budburst phenology and the interaction between light treatment and the height of the buds up the light cages was close to significance. Observations of the raw data (see figures 5.6 & 5.7) suggest that there is an apparent tendency for the high buds in the yellow light treatment to burst earlier; this may be due to the increased intensity of light, to which the oak are sensitive, at the top of the cage. Whilst the lux readings in the methods section indicate that the light intensity of the white light treatment is also increased at the top of the cage, lux is a measure of intensity as perceived by the human eye, and so if the wavelengths of light emitted by the white light treatment are not utilised/perceived by the oak, then the increase in the white light treatment's intensity is irrelevant. Intensity aside, given the mechanism by which phytochrome receptors enable plants to effectively determine day length, it is perhaps the ratio of different light spectra to which phytochromes are sensitive, rather than absolute intensity, that is more important (Linkosalo & Lechowicz 2006; Gaston *et al.* 2013). If artificial light at night were to advance budburst of oak and have no effect on winter moth egg hatch, one might expect this to cause closer synchrony between moth and host, as climate change is thought to have caused winter moth eggs to hatch too early to synchronise with oak development (van Asch *et al.* 2013). It may also be the case that synchrony would be adequately maintained between moth and host through a rapid evolutionary response of the winter moth egg hatching date; evidence suggests that winter moth egg hatching date has changed genetically,

under selection pressures from environmental change, to adequately maintain its synchrony with oak (van Asch *et al.* 2013).

Whilst oak and winter moth interactions make a good model system upon which to experimentally investigate some of the potential impacts of light pollution, particularly given the fact that there is some evidence to suggest that oak budburst may be affected by artificial light at night (Ffrench-Constant *et al.* 2016), the evidence from the present experiment suggests that low intensity light, lacking UV and far-red emissions, is unlikely to affect the system. Further experimental investigation, or field study, would be needed to rule out an effect of light pollution on the timing of oak budburst and winter moth egg hatch. It would also be interesting to investigate other biological systems that are perhaps more likely to be subject artificial light at night, such as those that are found lower to the ground, or on road verges directly beneath street lighting, in order to better understand how species interactions could be affected by street lighting.

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Figures

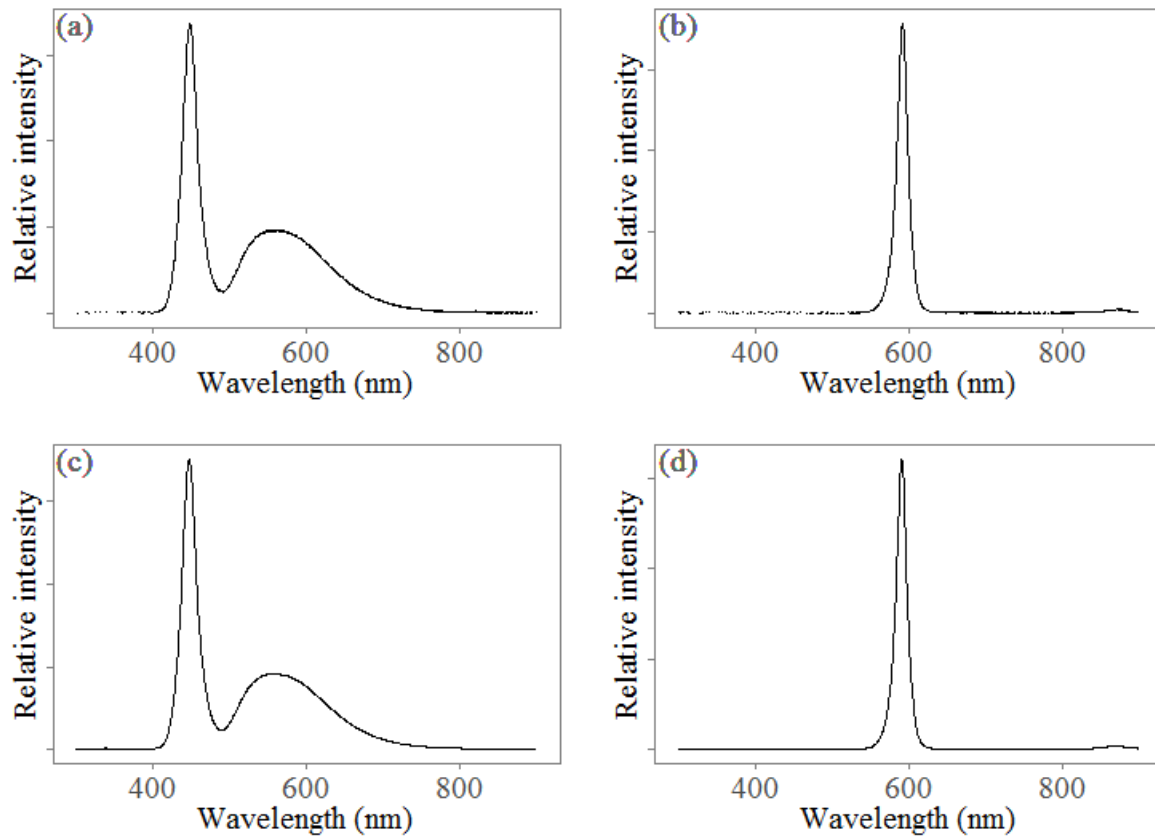


Figure 5.1: Spectral energy distribution of the lighting used for the study (a) Cool white LED (reading taken through petri-dish lid) (b) Amber LED (reading taken through petri-dish lid) (c) Cool white LED (d) Amber LED (reading taken without petri-dish lid). Spectral energy data were measured in the field during the hours of darkness using an Ocean Optics Maya 2000 spectrometer.



Figure 5.2: Photograph of experimental setup: The image depicts the block of 18 light cages (6 x white, 6 x amber and 6 x dark control cages), within which the oak saplings and winter moth ova were positioned. The dark panels on the sides of the illuminated cages prevent light spill into neighbouring cages; baffles along either side of the LED strips prevent light spill in the other direction.



Figure 5.3: Photograph of the stage of bud development at which buds were deemed burst; during the present experiment budburst was recorded as having occurred when buds reached the stage development depicted by the uppermost bud in the above photograph.

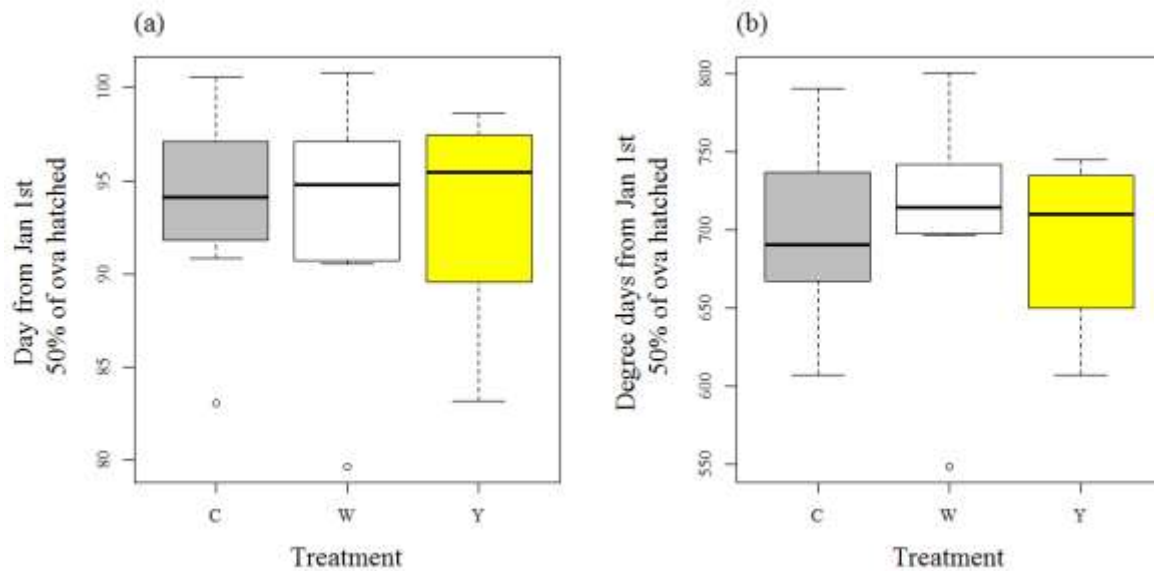


Figure 5.4: (a) Relationship between the mean date (day of year) per cage on which 50% ova hatched and the different light treatments. Boxplot based on raw data of all sub-clutches of ova; $n=10$ sub-clutches per treatment. (b) Relationship between the mean accumulated degree ($^{\circ}\text{C}$) days per cage on which 50% of ova hatched and the different light treatments. Boxplot based on raw data of all sub-clutches of ova; C- $n=10$, W- $n=7$, Y- $n=10$. For both boxplots, C= dark control, W= white LED light treatment, and Y= yellow LED light treatment. Centre lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots.

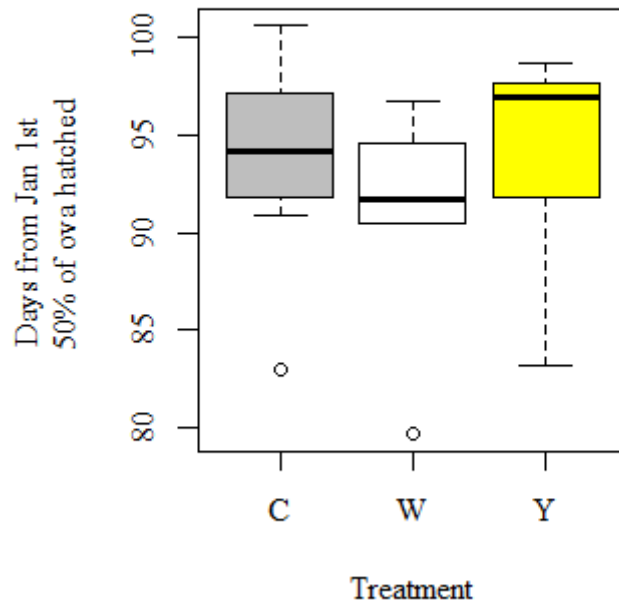


Figure 5.5: Relationship between the mean date (day of year) per cage on which 50% ova had hatched and the different light treatments in the cages that were not caused to malfunction by inclement weather. C= dark control, W= white LED light treatment, and Y= yellow LED light treatment. Boxplots based on raw data of all sub-clutches of ova; C- n= 10, W- n=6, Y- n=8. Centre lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, outliers are represented by dots.

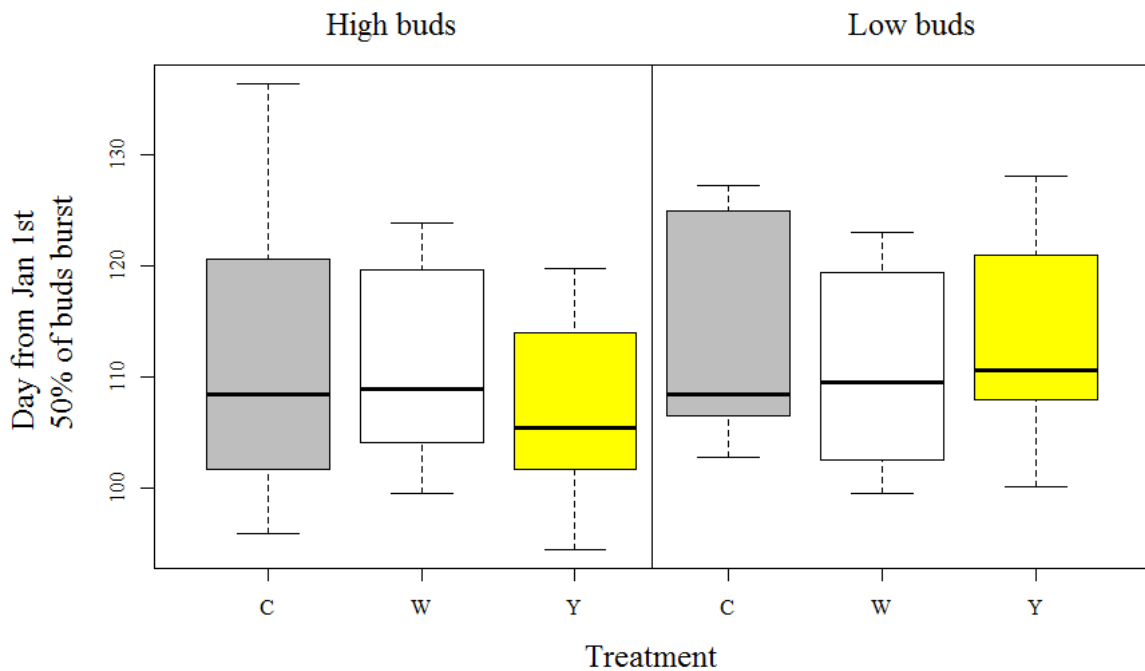


Figure 5.6: Relationship between the mean date (day of year) of 50% budburst, for high and low buds, and the different light treatments. C= dark control, W= white LED light treatment, and Y= yellow LED light treatment. Boxplot based on raw data of all individual trees; trees with high buds: C - n= 12, W - n= 5, Y - n= 9; trees with low buds: C - n= 9, W - n= 9, Y - n= 13. Centre lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles.

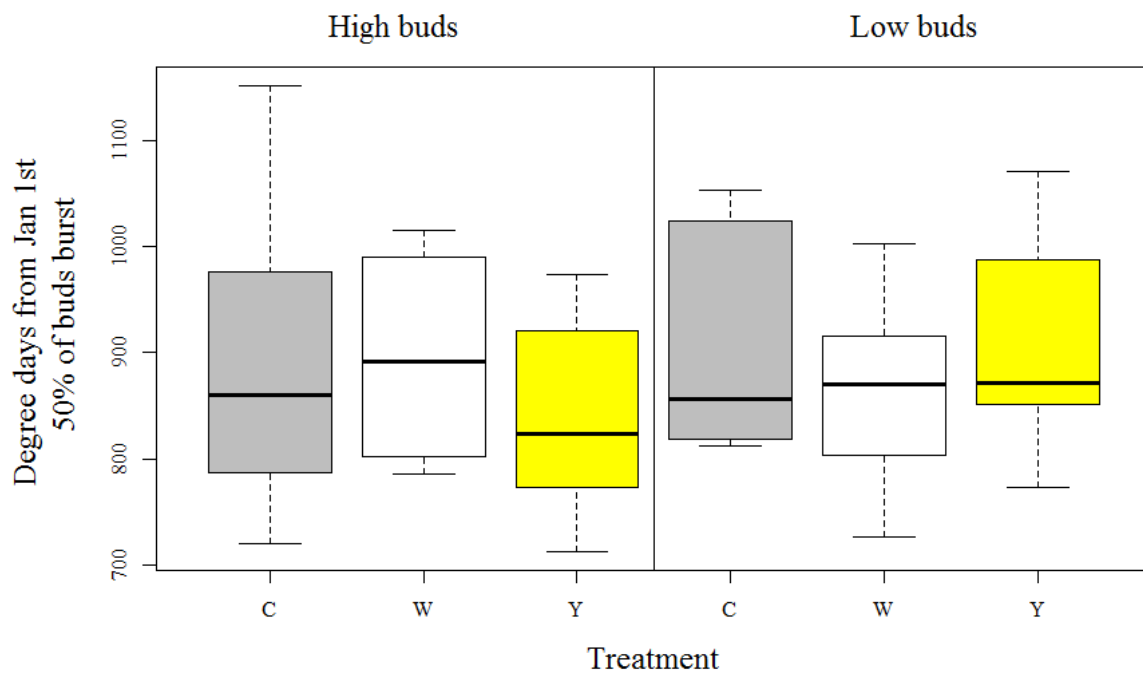


Figure 5.7: Relationship between the mean accumulated degree days ($^{\circ}\text{C}$) on which 50% budburst had occurred, for high and low buds, and the different light treatments. C= dark control, W= white LED light treatment, and Y= yellow LED light treatment. Boxplot based on raw data of all individual trees; trees with high buds: C - n= 12, W - n= 4, Y - n= 9; trees with low buds: C - n= 9, W - n= 7, Y - n= 13. Centre lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles.

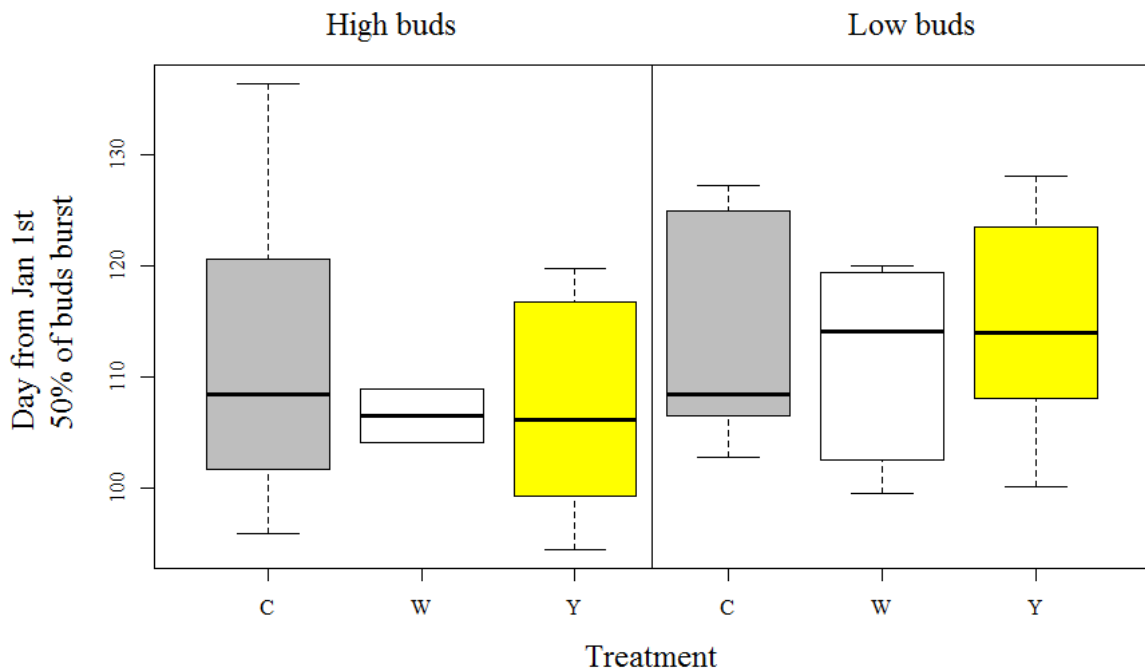


Figure 5.8: Relationship between the mean date (day of year) of 50% budburst, for high and low buds, and the different light treatments in the cages that were not caused to malfunction by inclement weather. C= dark control, W= white LED light treatment, and Y= yellow LED light treatment. Boxplot based on raw data of all individual trees; trees with high buds: C - n= 12, W - n= 2, Y - n= 7; trees with low buds: C - n= 9, W - n= 9, Y - n= 13. Centre lines show the medians; box limits indicate the 25th and 75th percentiles as determined by R software; whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles.

Chapter 6: General discussion

The initial objective of this project was to investigate the potential impacts of light pollution on moths, with a specific focus on, a new, ceramic metal halide street lighting that had recently been rolled out in Cornwall, UK. Although the project was prompted in part by the roll out of new street lighting in Cornwall, it was also timely at a broader scale, given the known importance the ambient light level to living organisms (Gaston *et al.* 2013) alongside a lack of knowledge on the ecological impacts of light pollution, the increasing amount of artificial night-time lighting globally (Hölker *et al.* 2010), a trend for the increased utilisation of more energy efficient lighting types such as LED (Pimputkar *et al.* 2009; Peters 2011), and the relatively recently documented declines in moth numbers.

Light pollution is potentially a very broad subject area in itself. For example, night-time lighting can vary in terms of spectra, intensity, amount (i.e. number of light sources), and duration (i.e. a flashing light or illumination throughout the night); it can be manifest as a diffuse reflected light through skyglow or as a bright point source direct from a lighting fixture, indeed, the physical structure of a lighting fixture, such as a street lamp, can have a bearing on the nature of the light it emits (i.e. the height of, or direction of emission from the light). The number of potential ways in which moths could be affected by artificial light are also numerous. Although it is likely that concern over light pollution's potential impact on moths is mainly due to their well-known 'flight-to-light' behaviour, which in itself could impact moths in many ways (Rydell 1992; Svensson & Rydell 1998; Frank 2006; Wakefield *et al.* 2015; van Geffen *et al.* 2015), there is also potential for night-time lighting to affect moths through artificial alteration of day length; photoperiod is known to play an important role for many organisms, including moths and organisms at other trophic levels with

which they interact (Basler & Körner 2012, 2014; van Geffen *et al.* 2014, 2015; van Geffen *et al.* 2015; Salis *et al.* 2016).

Whilst the number of potential consequences of 'flight-to-light' behaviour are many (i.e. direct mortality caused by the light, increased predation risk, disruption of necessary activities such as mating and feeding), in some ways, the severity of all of these consequences is governed by the strength of the 'flight-to-light' response, in terms of both numbers of moths attracted and the distance from which moths are attracted. Therefore, identifying lighting types which simultaneously meet anthropogenic requirements and reduce 'flight-to-light' behaviour was deemed a valuable focus for the current research project, especially given that artificial night time lighting looks set to stay, and as such limiting its impacts rather than eliminating them seems the most likely course of remediation. The project focussed predominantly on comparing different commonly or increasingly used types/spectra of lighting in terms of their attractiveness to moths. However, just because a lighting type reduces the impact of 'flight-to-light' behaviour on moths, does not necessarily mean it also reduces other potential impacts of artificial light on moths, caused by raised ambient night-time light levels. I therefore also investigated how different types of light could potentially impact on other aspects of moths' lives; as there was a paucity of studies looking at the impacts of different lighting types on moth and hostplant phenology, and thus their interactions, this was made a focal point. Both sets of experiments focussed on broad spectrum white light vs either narrower spectrum yellow/orange light, or yellow light lacking a significant UV component, as they are all lighting types known to meet the requirements of many common lighting applications, particularly street lighting. Although the focus on street lighting was, in part, prompted by the roll out of new street lamps in Cornwall, UK, it was also

deemed a particularly important type of lighting to investigate because it is one of the largest sources of artificial light at night (Luginbuhl *et al.* 2009).

Attractiveness of street lighting types to macro moths-chapters 2 and 3

Key findings

Chapter 2

The comparison of white, metal halide lighting with yellow, high pressure sodium lighting, in terms of their attractiveness to macro moths, was carried out as the metal halide lighting was comparable with the new street lighting, recently deployed in Cornwall, UK. The study revealed a number of interesting pieces of information. Firstly it revealed that the high pressure sodium lighting was less attractive to macro moths overall than the metal halide lighting, with the difference in lighting characteristics suggesting that this was likely due to the reduced UV light emissions from the high pressure sodium lighting (Rydell 1992; Kolligs 2000; Eisenbeis 2006; Eisenbeis & Eick 2011; van Langevelde *et al.* 2011a; Barghini & De Medeiros 2012). This finding was concordant with the findings of previous studies. Additionally, further analysis of the data revealed differences between the two major families of moth trapped during the study, in terms of their 'flight-to-light' response to the different lighting types. The aforementioned apparent 'preference' for the metal halide lighting overall, was almost entirely driven by moths of the Noctuidae family; moths of the Geometridae family were trapped in near equal numbers at both lighting types. There were also suggestions in the results of species specific differences in terms of relative attraction to the two lighting types, but it was deemed that further study would be necessary to firm up this finding.

The findings are useful in so much as they contribute to existing information, highlighting the fact that lighting types that emit UV are likely to be more detrimental to moths. They also highlight how the response of moths to different lighting types can vary, potentially even between species of the same moth family. This finding was deemed potentially useful as a possible means of understanding whether artificial night time light is contributing to the decline in moth abundance apparent across the UK and Europe. Given the results, and assuming that increased attraction to light results in increased moth mortality, one might expect noctuid populations to decline more steeply in areas where the predominant source of artificial light emits more shorter wavelength and UV than in areas where the light emits less UV and more longer wavelength light, whereas, geometrids would likely be similarly affected in both areas.

Chapter 3

Also a comparison of two street lighting types, the experiment described in Chapter 3 compared the attractiveness to macro moths of LED street lighting with that of ceramic metal halide lighting. The LED lighting was found to be considerably less attractive than the ceramic metal halide lighting, approximately six times fewer moths were attracted to the LED lighting; this was broadly concordant with the findings of most previous published studies, which show that LED street lighting, although variable in the degree to which it attracts insects, is generally one of the least attractive forms of lighting (Eisenbeis & Eick 2011; van Grunsven *et al.* 2014); but see (Pawson & Bader 2014). In contrast to the findings of chapter 2, no significant difference in terms of relative attraction to the two studied lighting types was found between the moth families, Noctuidae and Geometridae. However, although there was no statistically significant difference, there were indications in the data of a

difference that may or may not become apparent with further study; Noctuidae were predicted by the statistical model to be approximately seven times more attracted to the ceramic metal halide lighting than the LED lighting, whilst Geometridae moths were predicted to find the ceramic metal halide about twice as attractive as the LED lighting.

Challenges & considerations

There are a number of challenges associated with studying the attractiveness of street lighting to flying insects. First, and as previously mentioned, lighting types are extremely variable; the spectra of light emitted from street lights can differ greatly, as can the structure of the street lamp housing itself, which in turn can affect the way the light spills from the source. Therefore, without a vast budget it would be very difficult to make absolute conclusions about the most ecologically sensitive street lighting type. For the present study, the focus was on the spectra of the light emitted, rather than the structure of the street lamps; to avoid the impact of variation in street lamp structure on the attractiveness to moths, we constructed street lamp like structures that were physically as similar as possible, differing pretty much only in terms of the light they emitted. Having said this, our budget didn't allow for customization of the lamps and bulbs themselves, so we had to utilise 'off the shelf' lights. For the lights used in chapter 2, metal halide and high pressure sodium, this was not a problem, as we were able to match them identically in terms of their physical structure. For chapter 3 however, the LED lighting housing was structurally slightly different to that of the ceramic metal halide lighting; this was of particular concern as the lighting housings were integral to the moth traps used for the experiment. With hindsight and comparison of the results with the findings of others, our experimentation seems to have led to similar conclusions to those of others, but

this difference between lighting/moth trap structures theoretically does throw a little doubt over the scientific integrity of chapter 3. Another challenge posed by the experimentation for chapters 2 and 3 was trapping moths at a street lamp type structure. Although the traps used were effective, in retrospect I have learnt that there are better possible options that may have trapped moths in higher numbers and thus led to more in depth conclusions and detailed information on light attraction among macro moths; those used by Eisenbeis and Eick (2011) did not rely on the light structure to form part of the trap and could be easily deployed on existing street lights in the field.

Follow-up research

Given the known variation in light attraction amongst different taxa, the aforementioned results, highlighting variation in lighting type preference between moth families, are suggestive of a complexity in determining a 'Silver Bullet' lighting type that will be universally ecologically friendly. Indeed, completely eliminating the ecological impacts of light pollution through the manipulation of spectra may not be possible given that most types of modern artificial light, in terms of spectra and intensity, are known to or have the potential to affect at least some type of organism (Davies *et al.* 2017; Longcore *et al.* 2015; Nemeč 1971; van Geffen *et al.* 2015). However, with regards to reducing the impacts associated with 'flight-to-light' behaviour, whilst the degree to which different taxa are attracted to one lighting type over another does vary, the differences are not always so great, and there are overarching consistencies across taxa (Longcore *et al.* 2015). It may therefore be possible to identify a lighting type that is less attractive to the majority of invertebrates that exhibit phototaxis. Indeed, even though the findings of the present study indicate that Geometridae were similarly attracted to both metal halide and

high pressure sodium lighting while the Noctuidae were considerably more attracted to the metal halide, the high pressure sodium would still be the best lighting choice of the two for universally reducing light attraction.

Whilst there has likely been enough research done to assist in identifying street lighting types that would be less attractive to insects overall, extensive field study, to further pin down the relative attraction to different commonly used street lighting types, of different moth families or species, could be really useful in determining whether street lighting has had a role in the recent declines in moth abundance in the UK. Although artificial night-time light is known to have some detrimental impacts on moths, it's not known whether it is having a significant impact on moth populations. It would be useful to know whether night-time light is playing a role in the apparent decline in moth numbers, and thus know how much concern for moths is needed due to the proliferation of light at night. With confident measures of the relative attraction to different lighting types of different moths, data from the Rothamsted light trap network could be used to look for a relationship between the rate of moth abundance change, and the relative levels of attraction of different moth species to the main street lighting types at the locations of the Rothamsted moth traps. Given the results of the present analyses, less severe declines in overall moth abundance might be expected in areas where the predominant light source is LED, than in areas where metal halide lighting is found. In addition, declines of Noctuidae moths might be steeper in areas where metal halide lighting is the major street lighting type than in areas where the main source of lighting is high pressure sodium, while Geometridae moths may be expected to fare similarly in both areas. Other than through manipulating the spectra of street lighting to reduce the impacts of insect/moth attraction, which has been made more possible with modern LED

lighting, and has been researched fairly extensively (Barghini & De Medeiros 2012; Eisenbeis & Eick 2011; Longcore *et al.* 2015; Somers-Yeates *et al.* 2013; van Langevelde *et al.* 2011; chapters 2 & 3), the impacts of light attraction could also potentially be reduced through part night lighting. Many local authorities across Europe already employ part night lighting schemes, where lights are turned off for a period of time in the middle of the night as a means to reduce carbon emissions and energy costs (Bennie *et al.* 2014). Such measures could also potentially reduce the impacts of 'flight-to-light' behaviour on moths and other invertebrates, as flight activity can vary at different times of night (Beck & Linsenmair 2006). Research into the times of night at which 'flight-to-light' behaviour is at its lowest could be useful in determining when to switch off street lights. However, the switch off of street lighting is only likely to be possible when there is a reduced anthropogenic need for it, and thus, unless the peak flight time of moths and or other invertebrates coincides with a low demand for street lighting, switch-offs are likely to be ineffective.

There is little available information on whether artificial light at night, particularly in the form of rows of street lighting, acts as a barrier to the movement of moths in the landscape. It is known that moths that fly to light can settle near a light source for quite some time (Wolfling *et al.* 2016) , but the extent to which such behaviour acts as an effective barrier to movement is less clear. Further knowledge on whether street lighting does act effectively as a barrier to moth movement could be useful, as such information could be used to inform lighting designs, so as to maintain habitat connectivity. Mark-release-recapture techniques could be used to test whether rows of street lights act as a barrier to moth movement (Truxa & Fiedler 2012); releasing marked moths on one side of a line of street lamps and comparing their rate of recapture on the other side of the street lamps between trials with the lights switched

on and off could be used to do this. Harmonic radar, which can be used to track the flight of small insects in open environments (Svensson *et al.* 2001) could also be used to do this. Results from harmonic radar study could be particularly interesting as it could perhaps provide insight in to other ways in which ‘flight-to-light’ behaviour modifies the natural flight behaviour of moths. An attempt to use harmonic radar to study moth flight for the present research project proved difficult and costly; however, with more focus on this technique and with better access to the required facilities, harmonic radar could potentially provide some very interesting information about ‘flight-to-light’ behaviour in moths.

Effects of lighting on moth host plant phenology and moth host plant interactions- chapters 4 & 5

Key findings

Chapter 4

Chapter 4 focused on the spatial relationship between oak budburst phenology and the amount of night time light pollution, using citizen science data on budburst and satellite imagery of night-time light. The study was carried out because the timing of certain seasonal biological events can be extremely important, as often organisms at one trophic level are required to synchronise their lifecycle with those at another. The winter moth, for example, needs to match the timing of its egg hatch with oak budburst as the caterpillars feed on the oak buds; hatch too early and they may starve, hatch too late and they will be faced with less digestible leaves. In addition, there were very few studies, at the time of carrying out this experiment, focussed on the impacts of nighttime light on phenology and species interactions; particularly, none, to the best of my knowledge, focussing on the potential impact of light pollution

on the timing of phenological events at such a large spatial scale. The analysis revealed some particularly interesting results.

A UK wide dataset containing 13 years' worth of citizen science collected, spatially referenced oak (*Quercus robur*) budburst dates was matched with satellite imagery of night-time lighting and average spring temperature data, and the relationship between the variables was analysed. The analysis revealed that bud burst occurred earlier in brighter areas. The same result was found when the analysis was repeated on data points that fell outside of large urban areas; this was done to determine whether the urban heat island effect was causing the apparent relationship between the amount of light at night and the timing of budburst. The fact that the relationship was still apparent when analysing the data points outside of large urban areas reinforced the likelihood that the artificial night-time light was the driver behind the apparent advance in budburst in brighter areas.

Chapter 5

Chapter 5 describes an experimental follow-up to the aforementioned spatial analysis of oak budburst timing in relation to the amount of artificial night-time light. Oak (*Quercus robur*) saplings and winter moth (*Operophtera brumata*) ova were exposed to one of three experimental light treatments designed to replicate real world low level lighting conditions; a yellow light at night treatment, a white light at night treatment and a naturally dark control treatment. The saplings and ova were exposed to the treatments over part of the winter; from the 19th of December and 30th of January respectively, until the experiment was complete. In contrast to the findings of the spatial analysis, no statistically significant relationship between the light treatments and the timing of budburst was found. In addition, there was a non-

significant relationship between light treatment and the timing of winter moth egg hatch timing.

Challenges and considerations

Both the previously summarised chapters provided a number of contrasting challenges. The use of large data sets for the spatial analysis was great for picking out signal in a noisy study system, but the fact that the data was not collected specifically for the present analysis, and the fact that spatial resolution of the temperature and light pollution data were relatively coarse, meant there was some doubt over the precision of the predictions from the models fit to the data.

Conversely, the experimental setup, whilst far more controlled, in hindsight, would have benefitted from a higher number of replicates; given more resources and time this would have been possible. Furthermore, the experimental light cage experiment was further hindered by a failure to capture any winter moth females and thus their ova; this came down to a lack of prior experience in capturing the flightless female moths, and thus the experiment could be improved upon with the knowledge gained by contacting the research team in the Netherlands who were experienced in this, and who were fortunately able to provide moth ova for the experiment.

Follow-up research

To further study the winter moth and oak system, and how it is affected by light pollution, a large scale field study may be useful. A large number of sites at which mature oak trees are located, covering a range of different light pollution scenarios could be selected; at each site, both the phenological and abiotic measurements could be made. Winter moth ova would need to be gathered from female moths and positioned at each of the field sites, and their phenology measured alongside that of the oak. A field experiment such as this would result in a similar analysis to that

carried out for the spatial analysis described in chapter 4, but would allow for precise measurements of light levels and temperature to be made at the exact location of the study trees and ova. Such an experiment would also avoid the problem of using saplings, as mature trees could be studied; saplings are known to unfurl their buds earlier and respond differently to environmental cues than their mature conspecifics (Vitasse 2013).

As mentioned previously mentioned in the thesis, host plant species other than oak, which tend to be found more frequently in the vicinity of street lights are perhaps more likely to be impacted by light pollution. Blackthorn, upon which feed a number of moth and butterfly species, often grows in hedgerows which are frequently subject to street lighting, and as such may make a good study species.

Concluding remarks

Studies into the impacts of light pollution on individual species or other specific taxa, like those carried out for the present research project on moths, will likely be useful for certain situations, where, for example, the specific taxon in question is particularly endangered in a certain location. Information from such specific study will also contribute to the broader knowledge on the ecological impacts of light pollution, where it can be used in conjunction with the findings of other studies to inform universally ecologically sensitive lighting solutions. However, in terms of future research, more community wide study may be a more useful avenue, especially given that light at night can impact upon things other than the ecology of wildlife, such as human health (Navara & Nelson 2007). The 'Ecolight' project at the University of Exeter in the UK and the 'Lichtopnatuur' project at Wageningen University in the Netherlands are two large scale projects with a fairly broad focus; both are looking at wildlife communities and multiple aspects of ecology, in terms of

how they are impacted by artificial light; the 'Lichtopnatuur' project in particular is experimenting with a number of novel lighting types, of varying colours, as a means to identify particularly nature friendly types.

Further research into the impacts of light pollution is important, especially given the recent increased use of broader spectrum white lighting technologies over older, narrower spectrum lighting such as low pressure sodium. There is however, enough evidence already to determine that it will be near impossible to create a lighting type that would adequately function as street lighting whilst having no impact on ecology, especially given the many, as yet unidentified, ways in which light pollution could potentially impact organisms; particularly those caused via mechanisms other than phototaxis. Therefore, no lighting where possible would likely be the best option. Light lacking UV and shorter wavelength light would be better for reducing the 'flight-to-light' response of many invertebrates, as is evidenced in part by some of the findings of the present research project, and theoretically the narrower the spectra of a light source, the less likely it is to be usefully perceived by organisms at night and thus the less likely it is to alter the natural balance of species interactions at night (Davies *et al.* 2013).

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Annexed documents: publications stemming from thesis chapters

Annex 1: Somers-Yeates, R., Hodgson, D., Mcgregor, P.K., Spalding, A. & Ffrench-Constant, R.H. (2013) Shedding light on moths : shorter wavelengths attract noctuids more than geometrids. *Biology letters*, 9.

Publication stems from thesis chapter 2. Available from:

<http://rsbl.royalsocietypublishing.org/content/9/4/20130376.short>

Annex 2: Ffrench-Constant, R.H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., *et al.* (2016) Light pollution is associated with earlier tree budburst across the United Kingdom. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 283.

Publication stems from thesis chapter 4. Available from:

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