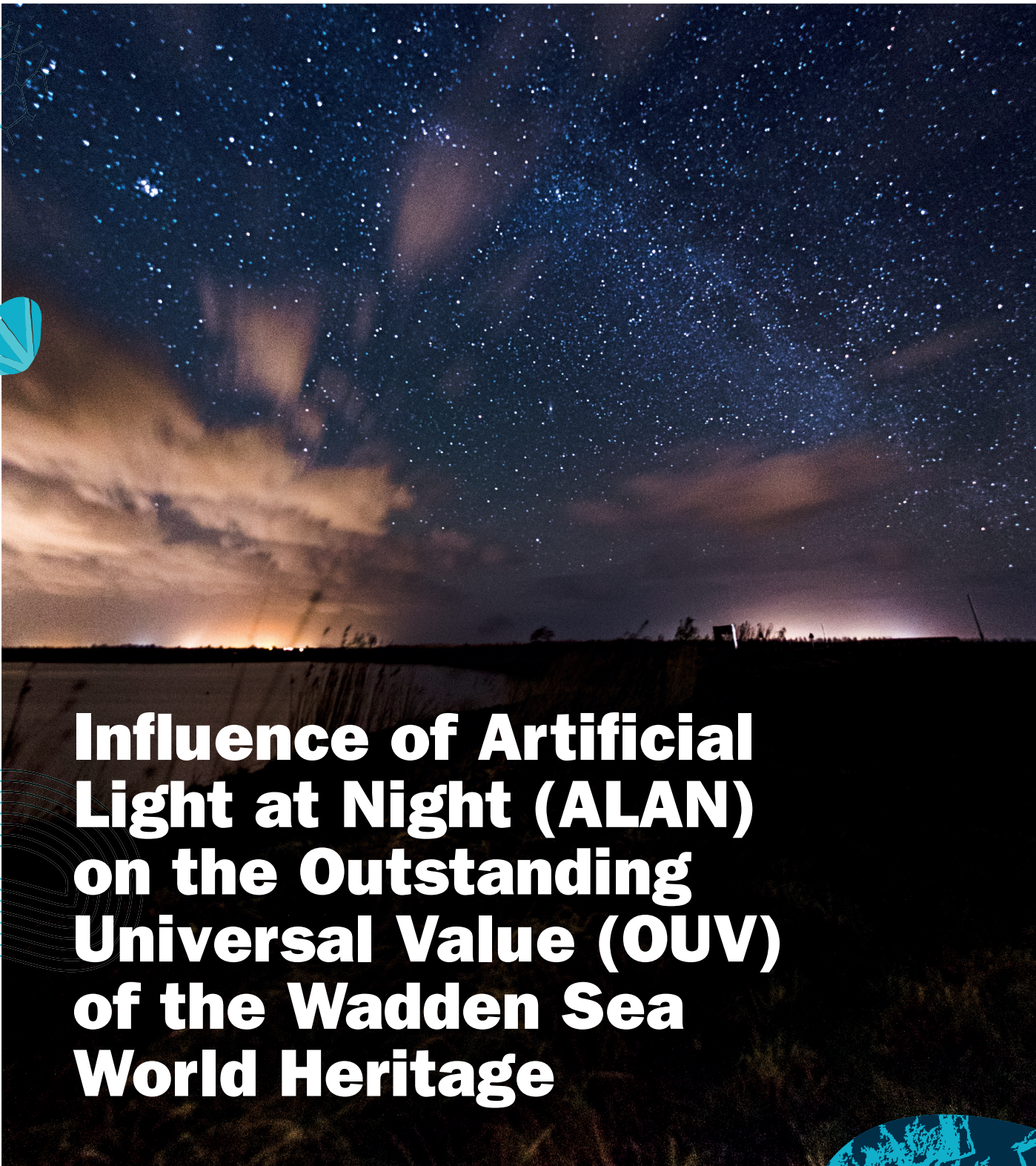


PROGRAMMA **NAAR EEN
RIJKE WADDENZEE**



**Influence of Artificial
Light at Night (ALAN)
on the Outstanding
Universal Value (OUV)
of the Wadden Sea
World Heritage**


Annette Krop-Benesch

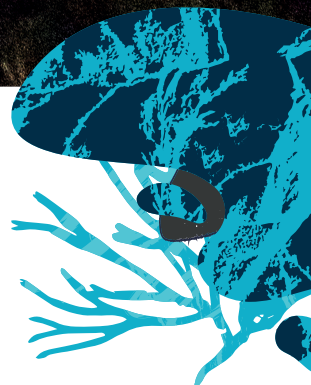
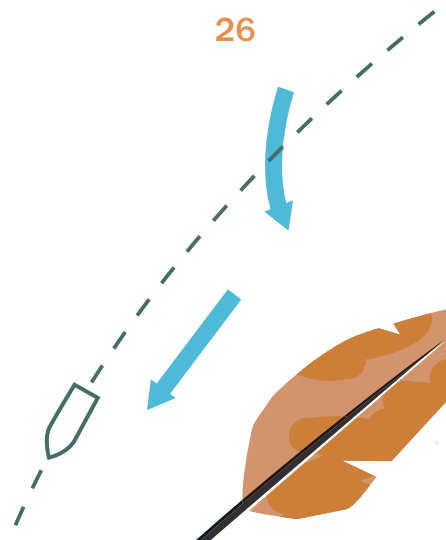
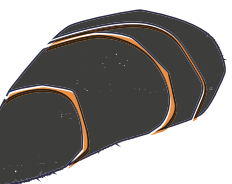


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1. Summary

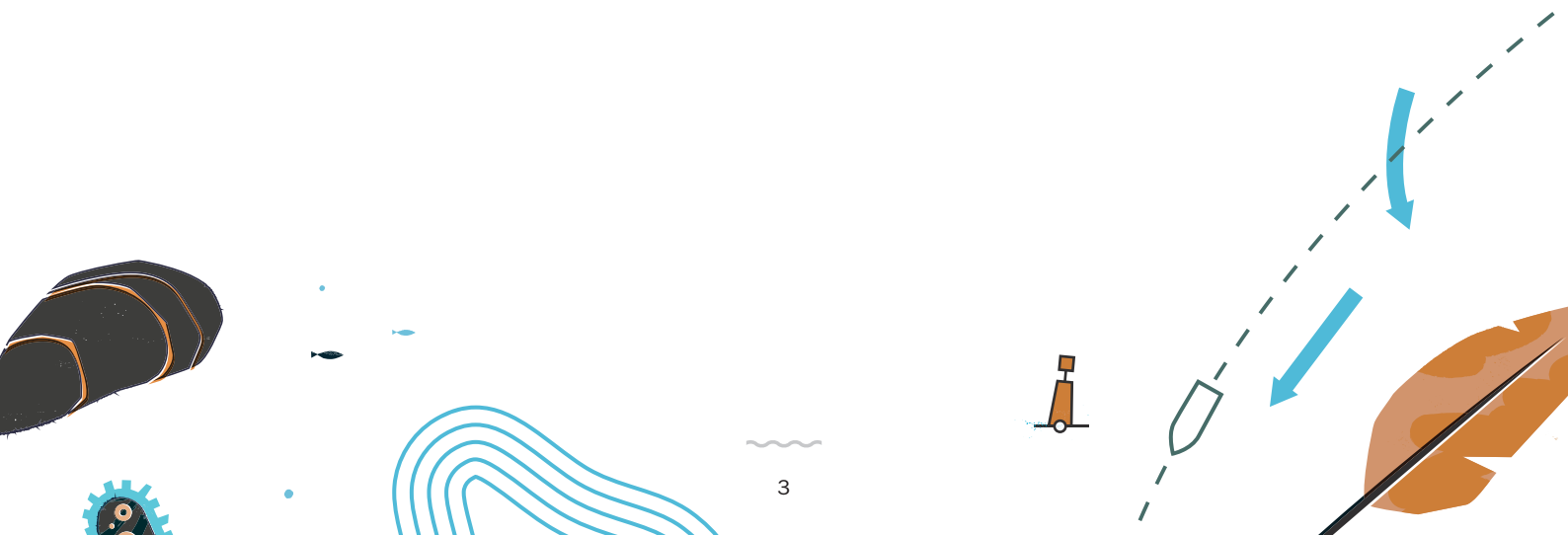


Artificial light at night (ALAN) is a growing factor in the anthropogenic environment. While light is generally seen as positive, there is mounting evidence that ALAN changes behaviour, space use, migration, physiology, development, and reproduction in almost all organism groups, including plants and microorganisms.

Special focus of research so far has been on birds and insects. The Wadden Sea World Heritage area is an important part of the East Atlantic migration route, with up to 12 million birds present over the year. ALAN has shown to change flight paths by attracting birds, thus posing a high risk of fatal bird strikes to millions of birds worldwide each year. Insects are also attracted to light sources and ALAN changes reproductive behaviour, which results in local reduction of insect populations. In all terrestrial ecosystems, insects play a vital role, and individual consequences have been shown to translate through cascade-effects into food webs and entire ecosystems. We also expect that the effects of ALAN on the barrier islands and coastal areas will translate to the intertidal habitats.

Less is known about the impacts of ALAN on marine ecosystems, but freshwater habitats have been shown to be especially sensitive to ALAN. Even low light levels are enough to interfere with fish hormone production, suppress plankton movements, and influence algal growths. In regard of marine and intertidal habitats, many questions still need to be answered, however, it is clear even now that ALAN is a serious environmental stressor. It most likely weakens the resilience of individuals and ecosystems to other stressor like climate change or chemical pollutants, exponentiating this damage.

Based on current evidence, ALAN needs to be used with care, especially in areas with mostly unchanged biological processes. Generally, the use of ALAN needs to be justified by balancing benefit and harm. Where ALAN is needed, there are light planning criteria to create illumination that reduces harmful effects to the environment. This document will summarise the known effects of ALAN on organisms and ecosystems in the Wadden Sea area or comparable habitats, of which some examples are shown in figure 1, and give brief recommendations how to mitigate these effects.



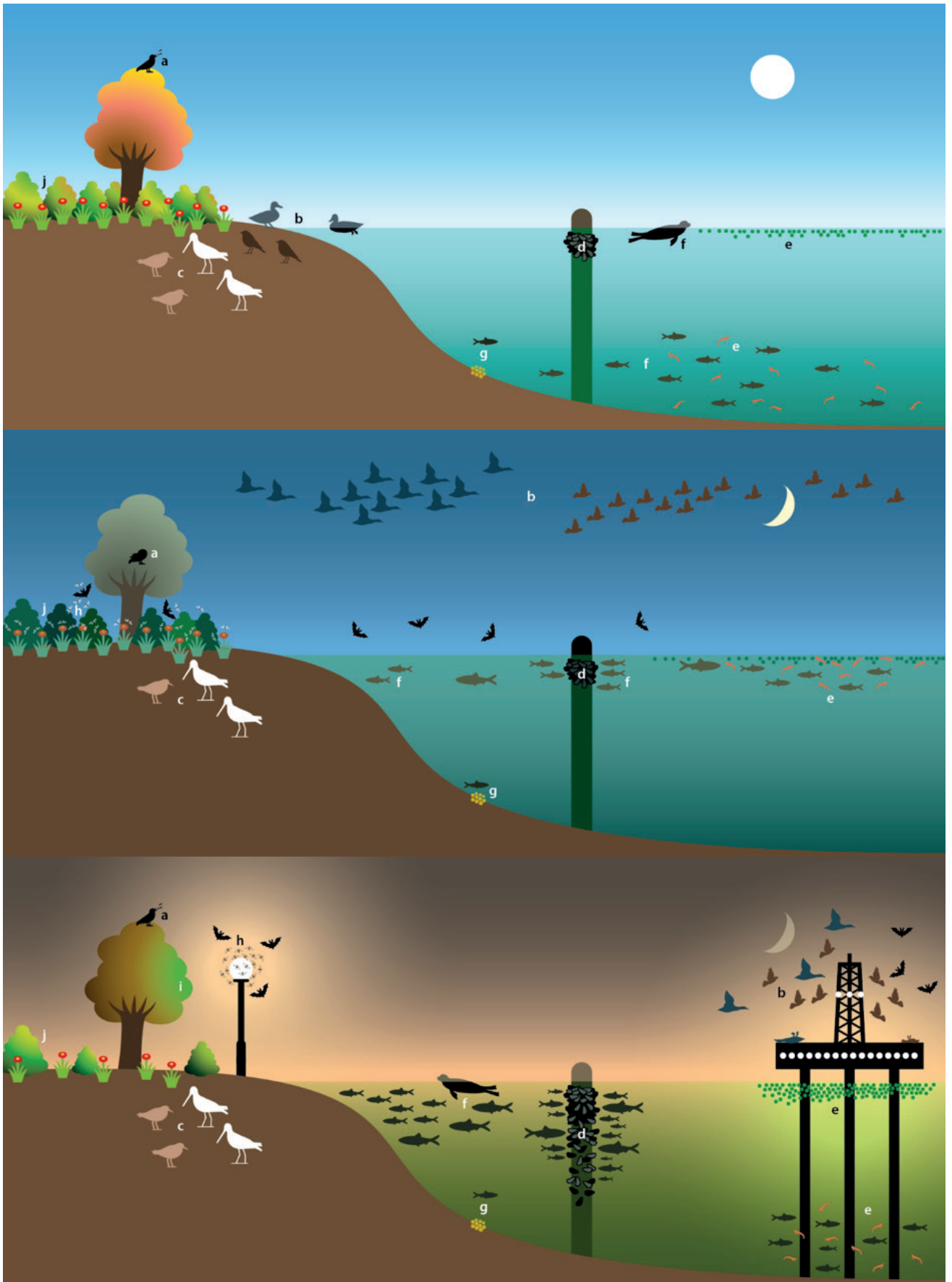


Figure 1: Summary of documented and expected effects of ALAN on organisms in the Wadden Sea World Heritage area.
Graphic by Annette Krop-Benesch and Michael Melchinger.

- (a) Songbirds usually sing during the day and rest at night. With ALAN, singing is extended into the night hours and sleep is reduced. ALAN also changes bird physiology and reproduction success.
- (b) Migratory birds rest and feed during the day and fly at night. Strong light sources at night attract birds and can cause bird strike. Migratory bats crossing the sea are also attracted to lights.
- (c) Visually foraging waders are more active during daytime than at night. ALAN allows them to extend foraging time. Tactile foraging waders show smaller difference between day, night, and ALAN.
- (d) Reef-building organisms like mussels and polychaetes choose the site of settlement due to light levels. With ALAN, they might settle in lower water levels than their usually habitat.
- (e) Starting with dusk, zooplankton, and small fish ascend from lower water levels to the surface to feed on phytoplankton. ALAN suppresses this diel vertical migration, reducing the transport of biomass to lower water levels. Phytoplankton biomass might increase due to extended photosynthesis.
- (f) Visually foraging fish, especially bigger species, are active, some smaller fish stay in lower water levels. ALAN increases fish activity during the night, increasing feeding pressure on prey species like reef organisms, but also increasing predation risk on smaller fish. Many fish species aggregate in the light, and harbour seals use this light for hunting.
- (g) ALAN can increase activity in fish species with parental care, wasting parts of a carefully rationed energy budget.
- (h) At night, moths and other nocturnal insects pollinate plants. ALAN draws these insects to light sources where many of them die, partly due to increased predation by bats. Consequently, pollination is reduced. ALAN also interferes with insect physiology and reproduction.
- (i) Plants use daylength to control seasonal rhythms, i.e. shedding of leaves. Trees under influence of ALAN keep green leaves until late autumn.
- (j) As a consequence, ALAN can lower the density of dune-forming plants.

2. Introduction



It has become customary in many parts of the world to use artificial light at night, so called ALAN, for various reasons in our outdoor environment. It allows activity and is used for decorative and advertising purposes. While artificial light at night (ALAN) has many advantages for human society, it has also been identified as a growing environmental stressor. About one third of vertebrates and two third of invertebrates are nocturnal. Natural light levels are an essential characteristic of every habitat, and loss of natural darkness can result in degradation of habitat quality (Hölker et al. 2010a; Kyba and Hölker 2013; Gaston et al. 2017).

Despite concerns about energy-consumption, the increase of global emissions of ALAN has been estimated as 2-6% each year (Hölker et al. 2010a; Kyba et al. 2017; Sánchez de Miguel et al. 2021). The actual increase might be higher, since these estimates are based on VIIRS satellite data, which is close to zero for light below 500 nm wavelength (blue light). In recent years there has been a wide-spread change from halide, mercury vapour, or sodium vapour lamps to LEDs with a higher content of blue light (see Figure 1), which is not measured by VIIRS. Thus, current data under-estimate light emissions to an undetermined extend. This is however significant, because LED lighting is favoured due to its energy-efficiency and will replace most other light sources (Sánchez de Miguel et al. 2021). Also, since running costs are reduced, in practice this often results in an increase of brightness and illuminated areas (Kyba et al. 2017).

The negative effects of ALAN are often referred to as light pollution. This form of pollution can act directly on organisms by locally increasing light levels and even momentarily blinding an animal with glare. It can also act over long distances as skyglow, a diffuse brightening of the night sky, which is mostly not consciously detected by humans but can be strong enough to interfere with the orientation and physiology of some nocturnal organisms (Moore et al. 2000; Kyba et al. 2011; Dacke et al. 2013; Kupprat et al. 2020).

The increase of ALAN in natural landscapes has led to concerns from researchers and organisations (UNESCO et al. 2009; Hölker et al. 2010a; Hölker et al. 2010b; Koen et al. 2018; IAU/UNOOSA 2020; IUCN 2021a; IDA 2021). During the last two decades, a growing number of studies has found detrimental effects of ALAN on organisms from basically all taxonomic groups and habitats. ALAN interferes with orientation, habitat use, biological rhythms, behaviour, physiology, reproduction, and health. Individual effects translate to the entire ecosystem, including changes in species composition and fragmentation of habitats. This holds for both nocturnal and diurnal species. Diurnal species may benefit from using ALAN to extend foraging time, but ALAN can also reduce sleep time and quality (Gaston et al. 2013; Gaston et al. 2014; Gaston et al. 2017; Koen et al. 2018; Ouyang et al. 2018; Grubisic et al. 2019; Sanders et al. 2021).

For these reasons, the use of artificial light needs a well-informed evaluation of benefits and damage. In this report, we focus on the known and possible impact of ALAN on the Wadden Sea World Heritage area. This area is recognised for its Outstanding Universal Value. It is the world's biggest intact intertidal ecosystem, with strongly intertwined geomorphologic and biophysical processes (UNESCO Criterion ix). in which reef-building and dune-structuring organisms play an important role. Intertidal ecosystems are highly rhythmic. The periodic changes in light intensity of the sun and moon are vital cues for these rhythms. Changes in biological rhythms have been shown to be detrimental for most taxonomic groups in all ecosystems.

The biodiversity of the Wadden Sea area is unusually high for coastal wetlands, with a prominent fauna of migratory and breeding birds, and a generally high production of biomass (UNESCO Criteria ix, x). ALAN has shown to be especially harmful for birds and insects (see chapters 5.1 and 5.2). It plays an important part in the current insect decline. Though there is growing research on the impact of ALAN on marine systems, relatively little is known about the impact of ALAN on intertidal systems. If no data is available on Wadden Sea species, we give information on species related to those native to those from the Wadden Sea or from comparable ecosystems. This allows assumptions and shows need for further research directly related to the Wadden Sea area.



3. Intact natural intertidal ecosystems



The Wadden Sea is the largest tidal flat system in the world, outstanding in its geomorphology and biodiversity. It connects exceptional terrestrial and marine ecosystems: the open North Sea to the tidal areas with the salt marshes, beaches and dunes. It is also influenced by estuaries, which have been considerably altered by human activities, but nonetheless remain a vital habitat especially for brackish-water species.

The Wadden Sea World Heritage is crucial as producer of biomass and sustains over 10,000 species of plants and animals. Its geological position and richness in habitats make it one of the most important areas for migratory birds, providing feeding and roosting sites for up to 12 million migratory birds.

The structure of the Wadden Sea is created by a unique interplay of physical forces on land (i.e., the dunes) and at sea (i.e., the offshore belt) and biological activities, for example the strengthening of these structures by reef-building organism or dune plants.

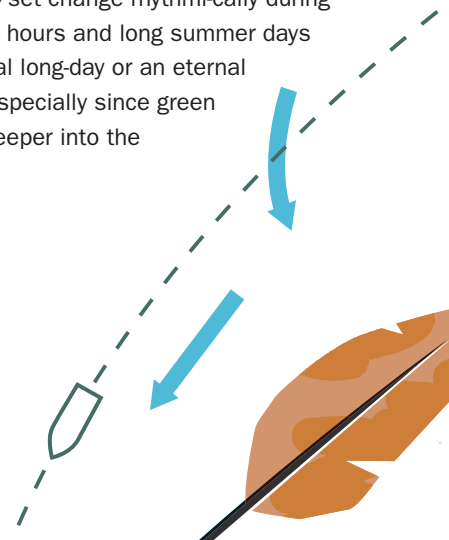
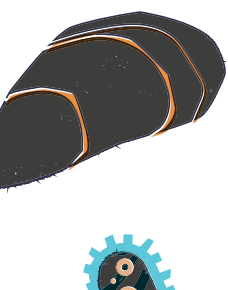
Everywhere on earth, life is shaped by the day-night rhythm, which is based on endogenous processes in the organism and synchronised to the environment predominantly through light. Seasonal rhythms are based on the rhythmic changes of these daily light rhythm.

In an intertidal system, organisms also need to follow the tidal movements of the water, which occurs twice every solar day with an interval of 12.4 hours. About every 15 days, there are semi-lunar maximal spring and minimal ebb tides when sun, earth, and moon become aligned at new and full moon. Thus, lunar cycles are important for inhabitants of the intertidal zone, too.

Tidal rhythms are easy to observe, even in larger animals. Harbour seals hunt for fish during high tide, and rest on sandbanks during low tide, while shorebirds now forage for food on the mudflats. Many invertebrate inhabitants of the tidal zone need to shelter during low tide from sun or predation and wait for the tide to return. Photosynthetic algae on the other hand use the low water levels to come to the top of the sand to harvest sunlight.

Intertidal species, such as corals, mussels, insects, and crustaceans have been shown to anticipate these rhythms and time locomotor activity, reproductive processes, and other behaviours accordingly. The midge *Clunio marinus*, which inhabits the tidal flats of the North Sea, synchronises larval development to ensure hatching during spring ebb (Wilcockson and Zhang 2008). There is evidence that this is regulated by a moonlight receptor in its eye (Fleissner et al. 2008). Tidal rhythms also interact with circadian rhythms, ensuring that diurnal activity peaks are synchronised with water levels (Wilcockson and Zhang 2008).

It is not clear how animals discriminate between moonlight and seasonal changes in daylength. Moonlight contains slightly less short wavelength (blue) light than sunlight, and intensity as well as time of moon rise/set change rhythmically during the lunar cycle. It is possible that this allows animals to distinguish between moonlit night hours and long summer days (Raible et al. 2017). ALAN could outshine these natural rhythms, either providing an eternal long-day or an eternal full moon scenario which would interfere with endogenous monthly and seasonal cycles, especially since green and blue light, which is a stronger component of artificial than of moon light, penetrates deeper into the open ocean (Davies et al. 2013; Davies et al. 2014; Davies et al. 2020).



4. Light in the Wadden Sea World Heritage



Natural light – artificial light: a comparison

Organisms are subject to immense daily changes in light levels (Figure 1), with daylight reaching an illuminance of 120.000 lx or more. During twilight, light is reduced rapidly. A moonless night can be as dark as 0,0006 lx, while moonlight reaches a maximum of 0,3 lx at full moon. Nocturnal light levels vary depending on cloud cover, presence of milky way and moon phase. Artificial light increases nocturnal light levels immensely, reaching local levels of more than a 100 lx and exceeding natural levels in approximately 88% of Europe's land surface (Falchi et al. 2016).

Artificial light also differs from natural light in terms of its spectral composition (Figure 3). Sunlight, which is seen as white light, contains all visible colours, UV light and infrared light. Moonlight is reflected sunlight in which some of the short-waved (blue) parts are reduced. Incandescent lamps have a high amount of long-wave light with very little short-waved light, resulting in the typical yellowish-warm light, while high and low pressure sodium lights emit mostly long-waved (orange) and near-infrared wavelength light. Metal halide and mercury vapor lamps on the other hand have several peaks and generally a high amount of UV and short-wavelength (blue) emission. LEDs have different spectral compositions, mostly differing in the amount of short-waved light ("blue content").

The impact of ALAN depends on the spectral composition of light. In most animals, short-waved light results in ALAN-related changes, however, some species react stronger on long-waved light (Longcore et al. 2018). Plants react on short-waved and on long-waved light (Bennie et al. 2016; Schroer and Hölker 2016).

Some animals also use polarised light. In polarised light, the majority of light waves are parallel to each other. This way, the light provides information on the position of the light source and can be used for orientation. Several insects, crustaceans, and some fish species use polarised light from moon, stars, and Milky Way (Schroer and Hölker 2016).

Artificial light can interfere with this information, diminishing the ability of nocturnal animals to navigate (Kyba et al. 2011). This has been shown in migratory birds, in which natural polarised light is needed for the magnetic compass (Muheim et al. 2016). Thus, there is no artificial light without ecological impact on at least some species.

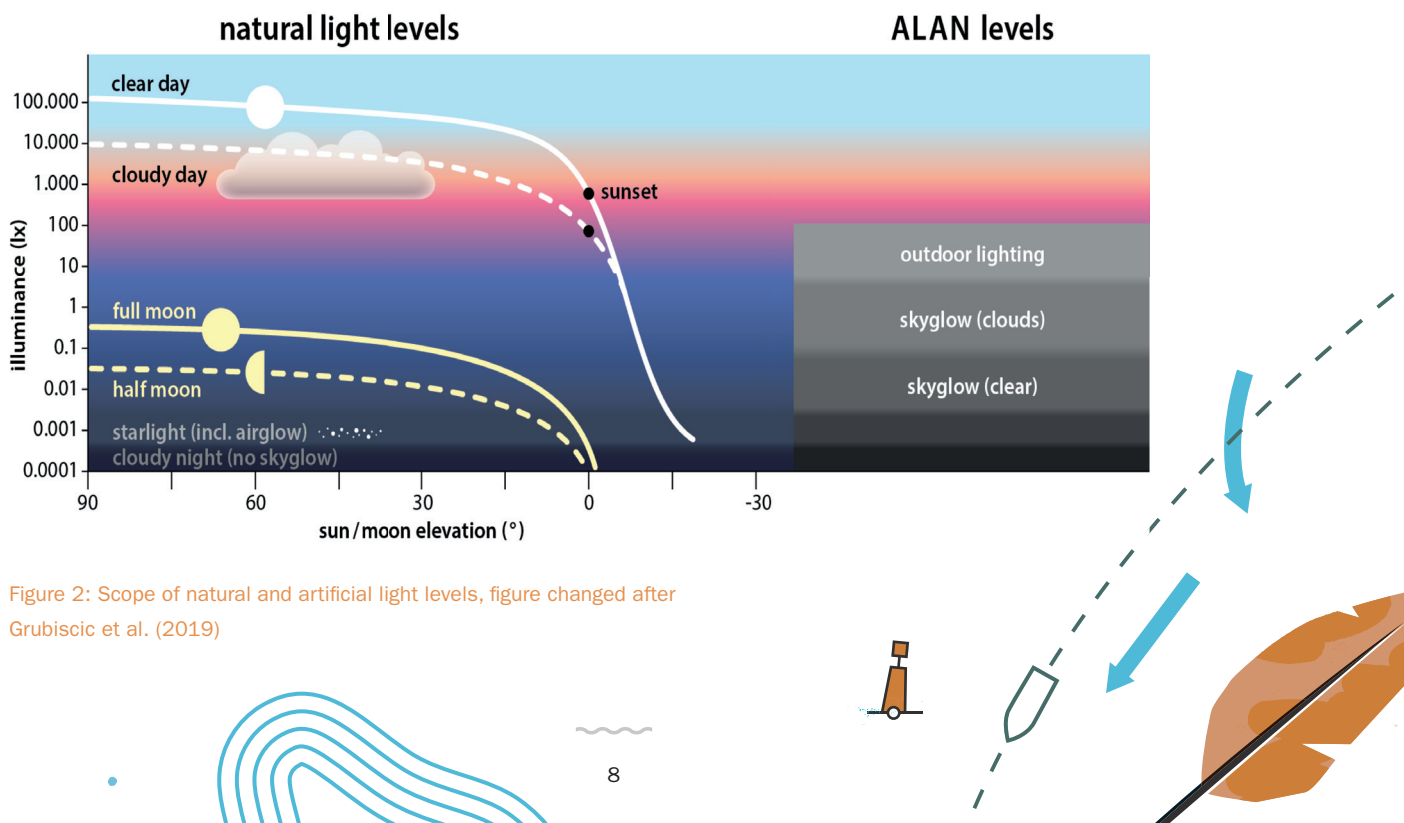


Figure 2: Scope of natural and artificial light levels, figure changed after Grubiscic et al. (2019)

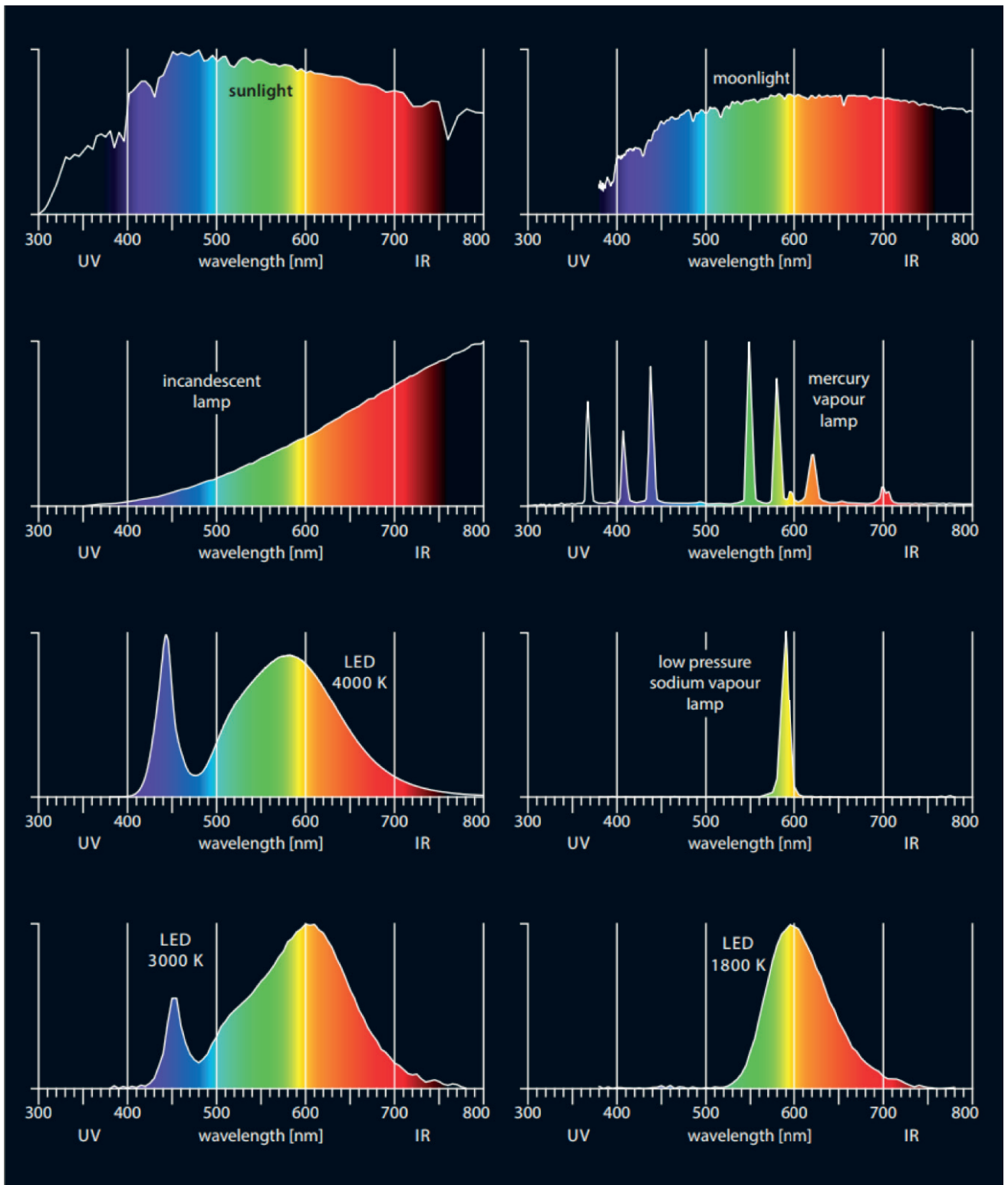


Figure 3: Spectral composition of light from natural and artificial light sources

ALAN in the Wadden Sea World Heritage

Though there are many efforts to protect the Wadden Sea World Heritage from ecological damage through pollutants, there has been little awareness on the impact of artificial light. Light emissions can reach over wide distances, thus crossing the borders. Without an established measurement network, the extent and changes of ALAN is hard to assess.

The Wadden Sea is subject to light emissions from coastal settlements, harbours, promenades, offshore platforms, offshore windparks, vessels, and greenhouses. Data from VIIRS satellites show how ALAN from the coast causes increased brightness throughout the entire Wadden Sea World Heritage (Figure 4). Harbours and industrial structures are sources of high emissions, even after work hours. Light can spill directly on the water and can be seen from bigger distances as skyglow (Figure 6). Such intense lights can attract nocturnal shorebirds and migratory birds (see chapter 1).

Light installations with less reach but considerable local impact are promenade lights (Figure 10) or path lights (Figure 11). There are also oversized security lights that are not restricted to the zone used by humans such as the payment machines at a beach shown in Figure 7 shows the night illumination of a campsite that spills into the neighbouring salt marshes, a zone protected from human trespass, but not from ALAN.

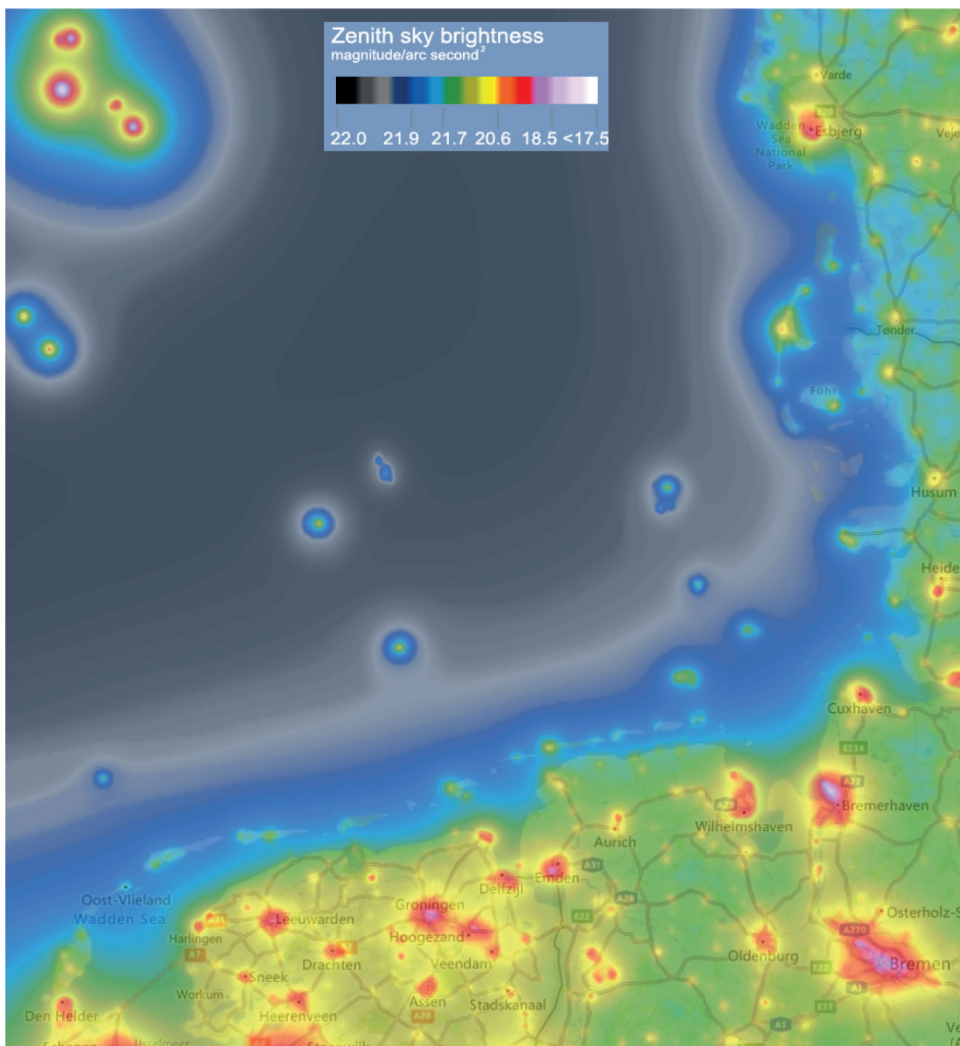


Figure 4: Light emissions at Wadden Sea World Heritage based on VIIRS annual World Atlas 2015 (Falchi et al. 2016), maps taken from www.lightpollutionmap.info

5. High biomass production, ecosystems, and the influence of ALAN



Primary producers

The fundament of every food web are photosynthetic bacteria, algae, and plants which transform sun light into carbon-based biomass. It might be expected that ALAN increases photosynthesis rate due to additional light. Indeed, at a Mediterranean coast an increase of biomass of photosynthetic bacteria was found (Maggi and Benedetti-Cecchi 2018; Maggi et al. 2020). On the other hand, ALAN has been shown to reduce biomass in freshwater periphyton (Grubisic et al. 2018b; Dananay and Benard 2018). It has also been shown that ALAN changes the diversity of the biofilm in favour of photosynthetic bacteria in marine (Maggi et al. 2020) and freshwater communities (Hölker et al. 2015), possibly changing the carbon and nutrient turnover. Such changes on the fundamental level of food webs can have widespread, so far unknown effects on the entire ecosystem and are highly undesirable.

Food webs

HABITATS AT THE UPPER WATER LEVELS

Primary producers are only found in the upper water levels which can be penetrated by light. They are either located as periphyton or sessile macroalgae at shores or reef structures or as drifting phytoplankton.

Periphyton is consumed by grazers, including snails, echinoderms, and fish. In a field study at a Mediterranean coast, an increase of photosynthetic biomass was compensated by increased grazing by the littoral snail *Melarhaphe neritoides* (Maggi and Benedetti-Cecchi 2018). In a longer study however, snail density decreased and bacterial composition changed (Maggi et al. 2020). It is possible that ALAN caused stress and elevated metabolic rates in these snails, resulting in increased food intake.

ALAN can also affect predators. The dogwhelk (*Nucella lapillus*), a predatory sea snail, shows more hunting behaviour in the presence of ALAN but is less likely to seek refuge at the waterline. Such immobility can be a sign of stress which might force the snail to hunt more to respond to increased stress-related energy demands (Underwood et al. 2017).

Many fishes are visual feeders that forage mostly during the day, so the night might provide sessile invertebrates with protection for feeding, settling, or spawning. ALAN has been shown to change fish behaviour, habitat use, and increase predation on sessile prey but might also increase predation risk for small and medium sized fish (Becker et al. 2013; Bolton et al. 2017).

Little is known about adult decapods like crabs, lobster, crayfish, shrimps, and prawns. They are keystone species that interact on multiple trophic levels and habitats: smaller species and larvae are part of the zooplankton, adults of bigger species inhabit tidal flats, estuaries and rivers. Crayfish species are regarded as mostly nocturnal. The signal crayfish (*Pacifastacus leniusculus*) is less active and spends more time in shelters under high pressure sodium streetlight (Thomas et al. 2016).

The reported changes in behaviour are signs of increased stress on individuals and communities and might result in altered energy needs, nutritional flux, and recycling of organic matter.



DIEL VERTICAL MIGRATION

The transport of carbon and nutrients into the lower, dimly lit water levels is being achieved by diel vertical migration (DVM). Organisms ascend to the surface during dusk and return to deeper water levels during dawn. In offshore waters, DVM can have an amplitude of up to several hundred meters, but DVM is also known from tidal waters and freshwater bodies. It has been observed in practically all taxonomic groups, from microscopic zooplankton to larger fish (Hays 2003) and is probably the largest daily migration of biomass on the planet (Davies et al. 2014).

The reasons for DVM are not fully understood but there is strong evidence that migrating species avoid visual predators while exploiting the rich food sources of the surface (Hays 2003). The guiding factor appears to be light, with ascend and descend taking place during twilight (Mehner 2012). Marine organisms have been shown to be guided by light levels as low as or even lower than moonlight (Davies et al. 2020). Light from boats is strong enough to induce an avoidance response from marine plankton (Sameoto et al. 1985; Ludvigsen et al. 2018), in freshwater *Daphnia*, even urban skyglow is strong enough to suppress DVM (Moore et al. 2000). Amphipods on the other hand have been shown to be attracted by light when in shallow water, with white LED light attracting more individuals and a different species composition than halogen lights (Navarro-Barranco and Hughes 2015). A disruption of DVM is most likely to result in reduced carbon and nutrient transport to lower water levels (Moore et al. 2000; Davies et al. 2014) but might also increase algae survival rates (Moore et al. 2000).

It is also interesting to consider how ALAN changes interactions between fish and planktonic prey species. Many fish are visual feeders, so ALAN might increase their foraging success. Consumption of invertebrate prey increased in the Eurasian perch (*Perca fluviatilis*) under dim light (Czarnecka et al. 2019). In rudd (*Scardinius erythrophthalmus*), foraging success depends on the spectral composition of the artificial light, with higher rates of prey detection under halogen light than under high pressure sodium light. This was matched by higher evasiveness of *Daphnia* prey, however, under metal halide, prey detection in rudd was still higher than in natural darkness, but *Daphnia* were less evasive (Talanda et al. 2018). The different reaction of taxa to light, i.e. the attraction of amphipods, can result in changes of community composition, thus changing the entire aquatic food webs (Navarro-Barranco and Hughes 2015).

In summary, ALAN changes foraging patterns and food distribution on many levels, potentially even disrupting biomass transfer from the surface to deeper water levels. This could result in fundamental changes of the marine food web.



Figure 5: Fishing boat with flood lights, photographed from the shore.
Photo Andreas Hänel.

Reef assemblages

Located next to the Wadden Sea, cold water reefs provide a habitat for a variety of organisms including the larvae of open water species. Other reef structures, even inside the Wadden Sea, are based on the Ross worm (*Sabellaria spinulosa*), a polychaete, and the blue mussel (*Mytilus edulis*). During the last 100 years these reefs have been in decline due to many factors. The geomorphological and ecological consequences of these declines are not understood yet.

Reef assemblages are structured vertically, with light intensity and spectral composition playing a role in the settlement zones of the different organisms (Thorson 1964; Davies et al. 2014; Davies et al. 2015). While most early stage pelagic larvae are photopositive, most change to photonegative later. Larvae often choose shaded locations for settling prior to metamorphosis. This choice of location is vital for survival and reproductive success, since water depth is linked to temperature, salinity, food resources, etc. (Thorson 1964), as well as to avoid competition with photosynthetic algae (Davies et al. 2014). ALAN might result in larvae settling too deep thus decreasing survival and reproductive success (Davies et al. 2014). Indeed, it has been shown in the UK that LED light can change the composition of marine epifaunal communities, with some species being more abundant in lit areas while colonisation by other species decreased (Davies et al. 2015).

For sessile organisms, synchronisation of gamete release is vital for successful reproduction. With prominent examples like the South Pacific palolo worm (*Eunice viridis*) it has been suggested that moon phases play an important role in this synchronisation for corals, polychaetes, and echinoderms (Davies et al. 2014). Sweeney et al. (2011) postulate that in corals not only intensity, but a combination with light spectra regulates this process. It has been shown that artificial urban air glow can indeed cause a mismatch in coral spawning (Kaniewska et al. 2015). More research is needed to understand the impact of ALAN on other taxonomic group and on feeding activity in general etc. Additionally, ALAN can increase predation on reef building organisms by grazing fish (Bolton et al. 2017).

ALAN in combination with other stressors might change and slow down reef assemblages, maybe even cause degradation of reefs. Little data is available on Wadden Sea species. however current knowledge is enough to call for caution to protect the geomorphological function of reef organisms.

Connections between marine and terrestrial ecosystems

There have been several studies showing how ALAN can change food webs, some on marine ecosystems (i.e., Bolton et al. 2017; Maggi and Benedetti-Cecchi 2018; i.e., Maggi et al. 2020), and many on terrestrial ecosystems (i.e., Manfrin et al. 2017; Bennie et al. 2018; Sullivan et al. 2019). Little is known about the connections between marine and terrestrial habitats.

Shorebirds connect these habitats, using terrestrial and marine resources, ALAN has been shown to change activity times in waders and herons (Santos et al. 2010; Dwyer et al. 2013; Tabor et al. 2017). As will be discussed in the next chapter, ALAN also changes flight patterns and habitat choice in migratory birds (McLaren et al. 2018; Horton et al. 2019). This might influence carbon and nutrient transport between marine and terrestrial areas. More research is needed to understand the interconnection of these ecosystems.

6. High biodiversity



Birds

The Wadden Sea is one of the most important wetlands for migratory shorebirds. It is part of the East Atlantic flyway and is used as moulting, overwintering, breeding area and for resting and feeding. On a yearly basis, approximately 10 to 12 million migratory birds use the rich network of habitats, including mudflats, estuaries, intertidal wetlands, sandy beaches, rocky shores, saltmarsh, wet grasslands, and ephemeral freshwater. Shorebirds also use pastures, tilled land, sewage treatment plants, irrigation canals, sports fields, and golf courses. Often large groups gather at single, productive sites. The Wadden Sea is also habitat for many seabirds like gulls, terns, noddies, auks, and shearwaters, many of these being endangered species. ALAN has been shown to be a stressor to birds in several ways, interfering with orientation, activity patterns, health, and physiology.

SHOREBIRDS BIRDS: CHANGE OF ACTIVITY TIMES

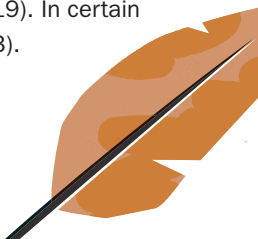
The intertidal habitat of shorebirds is not only subject to the diurnal day-night pattern, but also to the tidal rhythms. Shorebirds forage at night and day during low tide, preferring daytime foraging. This is especially the case in visual feeders like plovers, while tactile feeders like sandpipers can also forage at lower light levels and switch between visual and tactile foraging (Pendoley et al. 2020). ALAN could be useful for visual feeders, and indeed ringed plovers (*Charadrius hiaticula*), kentish plovers (*Charadrius alexandrinus*), grey plovers (*Pluvialis squatarola*), dunlins (*Calidris alpina*), and redshanks (*Tringa totanus*) use ALAN to extend foraging time and increase their prey intake, while the tactile-feeding avocets (*Recurvirostra avocetta*) show no differences. Though this is a direct advantage for the individual bird, it might result in a locally reduced density of invertebrates. ALAN might also draw waders into areas with greater human disturbance, higher rate of other pollutants, and higher predation risk (Santos et al. 2010; Dwyer et al. 2013).

MIGRATORY BIRDS AND SEABIRDS: ATTRACTION TO ALAN

Each year several million migratory birds pass through the Wadden Sea area, including shorebirds, ducks, geese, passerines, and many more taxa. Most of them, especially the passerines, travel during the night after taking directional clues during twilight. They are often encountered offshore during migration (Hüppop et al. 2019). Though the mechanisms of orientation are not fully understood, they use a combination of landmarks, celestial lights, and the earth's magnetic field. It is not clear if there is a hierarchy or interaction between these mechanisms. For nocturnal journeys, some migratory birds have been shown to use clues from sunset, others use star constellation for compass orientation. The magnetic compass also relies on light, it does not function in complete darkness, but needs the lighting conditions of a starry moonless night. It is to be expected that ALAN interferes with these mechanisms by changing polarity of the light or outshine the stellar constellations. There is also evidence that blue light is needed, while monochromatic red light can result in disorientation. However, independent from light colour, strong light can cause birds to orient into a wrong direction, especially in dark nights (Ballasus and Hill 2009; Chernetsov 2016).

Given the mechanisms of bird orientation it is not surprising that nocturnal collisions of migratory birds with illuminated structures are frequently reported (Hüppop et al. 2006; Ballasus and Hill 2009; Poot et al. 2009; Longcore et al. 2012; Longcore et al. 2013; Loss et al. 2015; Ronconi et al. 2015; Van Doren et al. 2017; Syposz et al. 2018; Rebke et al. 2019; Loss et al. 2019; Rodríguez et al. 2019; Zhao et al. 2020). It is not known how many birds are killed in Europe due to this. There are estimates of total bird mortality at oil and gas platforms in the North Sea as high as 6 million birds (Ronconi et al. 2015).

In North American it is estimated that 6.8 million birds per year are killed in collision with communication towers, which would be 2 to 4 times as many birds as killed by lead poisoning (Longcore et al. 2012) and up to 1 billion in collisions with buildings (Loss et al. 2015). Most bird fatalities with towers or buildings occur at night, during spring and autumn, and collision risk is correlated to the extent of illumination of the structure (Longcore et al. 2013; Loss et al. 2019). In certain species, fatal collisions could be experienced by more than 1% of the entire population (Longcore et al. 2013).



Nocturnality is also common in many seabirds, including petrels, shearwaters, noddies, and terns (Pendoley et al. 2020). Nocturnal behaviour is thought to be partly caused to avoid predation from larger predators. Watanuki(2014) reports a higher number of gulls during moonlight, while number of petrels was higher during darkness. It is possible that ALAN increases predation on petrels. Many seabirds, such as large gulls, shearwaters, storm petrels, and skuas, feed extensively on discards from fishery vessels. Feeding behaviour is similarly common during day and night, even in diurnal species, suggesting that the ship's strong lights have an advantage for these birds. Petrels might be able to use the light for foraging and then escape from predators by diving into the darkness (Garthe and Hüppop 1996).

While most of them are usually being pelagic, these birds come to the coast for breeding. Coastal lights can attract these birds into human settlements over many kilometres and cause them to ground. Due to their forward-heavy anatomy, grounded seabirds are often unable to take off again. They typically die from dehydration, predation, or car accidents. (Rodríguez et al. 2017b; Rodríguez et al. 2019). Adult Manx shearwater (*Puffinus puffinus*) on the contrary have been shown to avoid light near their colonies, which might result in decreased parenting behaviour (Syposz et al. 2021).

The attraction to ALAN is higher in moonless nights, with bad visual conditions (fog, clouds, most likely because birds cannot use stars for orientation), and in windy conditions (Ballasus and Hill 2009; Rodríguez et al. 2017b; Syposz et al. 2018; Rebke et al. 2019; Zhao et al. 2020). It appears that birds show avoidance behaviour from darkness and therefore fly towards the light. There are reports of several thousands of birds being attracted at the same time by a strong light source (Ballasus and Hill 2009).

The quality of light influences the strength of the attraction. Though one study (Poot et al. 2009) found the least attraction of migratory birds to blue and green light, several studies have shown that red light attracts significantly less seabirds and songbirds than green, blue, or white light. (Evans et al. 2007; Rebke et al. 2019; Zhao et al. 2020). Rodríguez et al. (Rodríguez et al. 2017a) found that short-tailed shearwaters (*Ardenna tenuirostris*) were more attracted to metal halide lights and white LED than to high-pressure sodium lights. Avoidance behaviour in adult Manx shearwater was also highest for white light, while red light had the least influence on bird abundance near the colonies (Syposz et al. 2021). A possible



Figure 6: Refinery port Wilhelmshaven (on the left) from 30 to 40 km.
Photo Andreas Hänel.

reason is that birds are less sensitive for red light and therefore show a weaker reaction. White light on the other hand might be a strong signal during dark nights. Despite being nocturnal, birds show avoidance behaviour to strong darkness, and the magnetic compass needs shortwave light for calibration. Birds might fly into the bright white light for orientation but are then blinded and trapped (Evans et al. 2007; Ballasus and Hill 2009).

Independent of colour, flashing lights also attract less birds than continuous lighting as has been shown at several buildings and communication towers and wind energy plants (Evans et al. 2007; Ballasus and Hill 2009; Rodríguez et al. 2017a; Rebke et al. 2019; Zhao et al. 2020). During the Tribute in Light event in New York, bird density increased shortly after lights were switched on, but birds dispersed soon after lights were switched off again (Van Doren et al. 2017). Short light intervals also reduced avoidance behaviour in adult Manx shearwater (Syposz et al. 2021). Thus current data on colour and light pattern suggests the use of red flashlights for wind mills, oil platforms, etc.

Birdstrikes might be the most obvious and dramatic consequence of the attraction to ALAN, but not the only one. Studies on migratory birds in North America suggest that migratory birds are attracted to areas with higher levels of ALAN, thus changing their natural migratory routes (La Sorte et al. 2017; McLaren et al. 2018; Horton et al. 2019). When trapped in a light beam, birds lose energy and need resting place close to the cities. These places might not be the most favourable sites for migratory birds. While attracted to light during flight, migratory birds avoid strongly lit areas when selecting resting sites, making it even harder to find suitable sites and increasing the density of birds at these places. As a consequence, birds might have to search longer for suitable sites or choose places that are less favourable. This could increase energy demands, put more pressure on chosen sites due to higher local bird densities, and heighten the risk of anthropogenic mortality (McLaren et al. 2018).

In summary, nocturnally flying birds are attracted to bright light sources for various reasons. This causes detours for migratory birds and fatal bird strikes. Though the extent of this is unknown, we can assume that it is a considerable strain for populations of migratory birds and seabirds in the Wadden Sea area.

SONGBIRDS: CHANGES IN PHYSIOLOGY

In songbirds, effects of ALAN on physiology, reproduction, and health have been shown. The most noticeable is an advanced start of the dawn chorus and an extended evening song for a variety of species in lit areas (Da Silva et al. 2015; Russ et al. 2015). There are also changes in reproduction: start of breeding is advanced in some bird species and delayed in others, also breeding success can be changed positively or negatively (Kempnaers et al. 2010; Dominoni et al. 2013; Senzaki et al. 2020).

Light levels as low as 0.3 lx have been shown to suppress melatonin production in black birds (*Turdus merula*) (Grubisic et al. 2019). This hormone controls the biological rhythms of birds and thus almost its entire physiology. Indeed, an increase in general activity, reduced sleep, increased levels of stress hormones, and reduced immune defence have been shown in adult and juvenile Great Tits (*Parus major*) (Ouyang et al. 2015; Raap et al. 2016b; Raap et al. 2016a; Ouyang et al. 2017; Raap et al. 2018; Grunst et al. 2020; Ziegler et al. 2021). House sparrows (*Passer domesticus*) and great tits confronted with ALAN also show less resistance to common infections (Ouyang et al. 2017; Kernbach et al. 2019; Kernbach et al. 2020).

These results suggest that ALAN could have long term effects on the fitness of many bird species. This can decrease resilience to other stressors such as chemical pollutants, diseases, or climate change. Species with higher plasticity for daylength on the other hand might have an advantage from ALAN, i.e., due to advanced breeding times in combination with climate change. Long-term studies are necessary to assess the impact on bird populations (Walker et al. 2019).

Insects, spiders, and other terrestrial arthropods

There have been warnings about a decline in insect populations in the Netherlands, Germany, and Great Britain (Hallmann et al. 2017; Kleijn et al. 2018; Hallmann et al. 2019), specifically in moths (Groenendijk and Ellis 2011; Hallmann et al. 2019; Coulthard et al. 2019). Though modern agriculture, pesticides, and habitat loss are accepted as the most important factors, light pollution has also been shown to impact insect populations (Wilson et al. 2018; Langevelde et al. 2018; Grubisic et al. 2018a; Coulthard et al. 2019), with declines in moth populations by 14 % within 5 years as reported by a Dutch study (van Grunsven et al. 2020), and a difference of numbers in moth caterpillars between lit and unlit streets of up to 52% in a UK study (Boyes et al. 2021).

Though there are only few insects in the intertidal environment, insects hold key positions in the coastal ecosystems. Not only do many plants rely on insect pollination, but insects also break down dead plant and animal material, and are prey for many invertebrates and vertebrates, thus providing valuable food sources. A decline in insect population is therefore a major concern for conservation.

ATTRACTION TO LIGHT

The most obvious impact of ALAN on insects is the attraction to light sources. Insects are drawn from their natural habitat, they waste time and energy, are not able to perform their ecological function, and might be killed, either by the heat of the lamp, by being trapped inside the luminaire, or as food for predators like bats and spiders.

It is not conclusively known why insects are attracted to the light, however, a number of studies has shown that UV-rich light as from metal halide and mercury lights is most attractive (Huemer et al. 2010; Eisenbeis and Eick 2011; Soneira 2013; Somers-Yeates et al. 2013; van Grunsven et al. 2014; Longcore et al. 2015; Wakefield et al. 2016; Wakefield et al. 2017; Martín et al. 2021; Brehm et al. 2021). It is less clear whether sodium lights (HPS and LPS) or LED are more attractive. Some studies found a higher attraction of sodium lights (Huemer et al. 2010; Eisenbeis and Eick 2011; van Grunsven et al. 2014), others found a higher attraction of LED (Pawson and Bader 2014; Wakefield et al. 2017). As described in chapter 3.1.1, LED lamps differ in their spectra, especially in their blue content. In Europe, LED with colour temperatures between 4000 and 3000 Kelvin (“neutral-“ and “warm-white”) are commonly used, with 1750 Kelvin (“amber”) LEDs in some places. The higher the colour temperature of these LEDs, the more short-waved light is emitted. Attraction of LED has been shown to increase both with colour temperature and blue content (Huemer et al. 2010; Longcore et al. 2015; Haller et al. 2021; Brehm et al. 2021).

Other important factors are light intensity and distribution. The higher the intensity, the more insects are attracted (Bolliger et al. 2020; Brehm et al. 2021). Attraction is reduced if light is directed downwards (Soneira 2013; Haller et al. 2021).

CONSEQUENCES OF ATTRACTION TO LIGHT

The high attraction of insects to light causes bottom-up effects in the food web. Spider webs show a higher density next to light sources, probably because catch rate is increased as consequence to higher insect abundance (Justice and Justice 2016; Mammola et al. 2018; Willmott et al. 2019; Parkinson et al. 2020). Some species reach maturity faster (Kleinteich and Schneider 2011; Willmott et al. 2019; Parkinson et al. 2020), but there is also evidence in some species of a higher mortality risk with high food intake (Marczak and Richardson 2008). However, some spiders species avoid light, probably experiencing food shortage since most insects are drawn to the light (Czaczkes et al. 2018).

Such local changes in the abundance of insects, e.g. due to attraction of flying insects to light sources, can either draw insects from their habitats or interrupt organism flux between ecosystems by creating a barrier. As a result, species-composition of ground-dwelling arthropods underneath the light sources is shifted towards predatory, light-tolerant or even diurnal species, with unknown consequences for the food web (Davies et al. 2012; Manfrin et al. 2017; Sullivan et al. 2019; McMunn et al. 2019).



Figure 6: Refinery port Wilhelmshaven (on the left) from 30 to 40 km.

Photo Andreas Hänel.

PHYSIOLOGICAL IMPACTS

In addition to the direct impact of attraction, light influences other behavioural and physiological processes. ALAN can reduce activity patterns in field crickets (*Teleogryllus commodus*), with possibly impacts on mate selection (Levy et al. 2021). Adult moths have been shown to reduce activity (van Geffen et al. 2015), food intake (van Langevelde et al. 2017), the production of pheromones (Van Geffen et al. 2015), and mating activity (van Geffen et al. 2015). ALAN can also impact body mass in moth caterpillars, in some species increasing it – which can be a sign for stress – (Boyes et al. 2021) in other species reducing it (Van Geffen et al. 2014; Grenis and Murphy 2019). Since larval development is timed by changes in daylength, it is not surprising that ALAN has been shown to affect entering of winter diapause in tiger mosquitos (Westby and Medley 2020), timing of eclosion in fruit flies (Thakurdas et al. 2009), and development time in crickets and moths (Van Geffen et al. 2014; Durrant et al. 2018).

For glow-worm populations, ALAN has been identified as the second-most threat worldwide (Lewis et al. 2020). LED and sodium street lights have been shown to reduce mate attraction success in the common glow-worm (*Lampyrus noctiluca*), possibly because the female's light signal is not detectable anymore by the males (Ineichen and Rüttimann 2012; Stewart et al. 2020; Van den Broeck et al. 2021; Elgert et al. 2021).

Such changes in physiology can reduce the fitness of individual insects as well as of the entire population and can at least partly explain the reductions in population size of 14 to 52 % reported in two studies (van Grunsven et al. 2020; Boyes et al. 2021).

In summary, ALAN influences many life stages of insects and other arthropods. The most prominent is the attraction to light that draws insects from their habitat, reduces population size, and diminishes their ecological function as food or pollinator. Less well studied but documented is the influence of ALAN on reproduction and larval development. Due to insects' ecological key position, these effects are transferred to the entire coastal ecosystem.

Fish

The Wadden Sea and its coastal areas are home to a vast number of marine and freshwater fish species, including the catadromous European eel (*Anguilla anguilla*) and Atlantic salmon (*Salmo salar*). Several fish species exhibit nocturnal movements between habitats, which might be driven by food abundance or predation. Light has been shown to be one of the major triggers for this migration (Neilson and Perry 1990; Mehner 2012) and some studies have found that diurnal migration cycles interact with tidal cycles (Wilcockson and Zhang 2008). However, most research is done during daytime, potentially leading to a wrong estimate about the utilisation and importance of different habitats (Hammerschlag et al. 2017).

CHANGES IN BEHAVIOUR AND SPACE USE

ALAN alters the abundance of fish in different ways, either increasing (Becker et al. 2013; Bolton et al. 2017) or decreasing it (Bolton et al. 2017). Many visual feeders use ALAN to detect prey, which is an advantage for bigger fish, but medium- and small-sized fish have to level the increased foraging success with higher risk of predation (Becker et al. 2013; Bolton et al. 2017) (also see 4.2).

ALAN can also increase general activity. Trinidadian guppies (*Poecilia reticulata*) kept under 0.5 lx were quicker to leave their refuge and spent more time in the open (Kurvers et al. 2018). ALAN also increased nocturnal activity in *Girella laevis* (Pulgar et al. 2019) and in smallmouth bass (*Micropterus dolomieu*) during parental care (Foster et al. 2016). Intermittent light as would be emitted from passing ships had an even higher effect than constant illumination (Foster et al. 2016). In *Girella laevis*, oxygen consumption was increased. Elevated activity that is not related to increased food intake would possibly result in higher energy demands and higher predation risk.

Juvenile salmonids (*Oncorhynchus* spp.) have been observed to be active in illuminated shorelines, with harbour seals (*Phoca vitulina*) and grey herons (*Ardea cinerea*), both visual hunters, preying on them (Yurk and Trites 2000; Tabor et al. 2017). European silver eels (*Anguilla anguilla*) instead avoid lit areas in a river and prefer unlit passages (Haddington et al. 1999; Cullen and McCarthy 2000). Such distractions from the usual migration route might lead to selection of unfavourable routes and loss of time.

HORMONAL CHANGES

If ALAN acts as a stressor, there should be changes in hormonal stress parameters. Several studies have tested for changes in cortisol without success (Brüning et al. 2015; Pulgar et al. 2019), but though sodium streetlights and car head lights did not result in elevated cortisol in bonefish (*Albula vulpes*), it did result in increased blood glucose levels, a result of elevated cortisol (Szekeres et al. 2017).

Melatonin production, which regulates the circadian activity rhythm of vertebrates, can be suppressed by very low light levels in some species. One lux is enough for a significant suppression in a variety of marine and freshwater fish species, for some species even the light of the full moon or urban skyglow can significantly reduce melatonin production (Grubisic et al. 2019). Reduced melatonin levels as well as increased stress levels can negatively impact on general fitness of an organism.

REPRODUCTION

Production of several reproductive hormones (i.e., LH, FSH, and sex steroids) has been found to change in European perch at levels of 15 lx (Brüning et al. 2018). Since there is evidence of lunar rhythms in some fish species for sex hormones, it is possible that much lower light levels can influence reproduction in some species (Fukunaga et al. 2019).

ALAN can also influence the development of offspring. In some freshwater species, egg development is accelerated, in others slowed down by ALAN (Brüning et al. 2011). In the common clownfish (*Amphiprion ocellaris*), eggs developed with normal speed, but there was no hatching at all under ALAN. Larvae hatched after the fish returned to natural light cycles (Fobert et al. 2019). Survival rate of juvenile orange-fin anemonefish (*Amphiprion chrysopterus*) was reduced by 36 % in the presence of coast-derived ALAN (Schligler et al. 2021).

To sum up, ALAN influences the behaviour, physiology, and reproduction of many fish species. We have to be cautious to transfer data on freshwater species on marine species, however, there are parallels in physiology that allow the conclusion that even low levels of ALAN are problematic for fish. This in combination with data on other marine species urges for more caution when using light on the water.

Amphibians

Amphibians are not some of the characteristic animals of the Wadden Sea, nonetheless they find habitats on the barrier islands and in mainland wetlands and are prey to many coastal birds. According to IUCN, Amphibians are the most threatened vertebrate class, with 40 % of species threatened with extinction (IUCN 2021b). Since amphibians rely heavily on insects as food source, they are affected by their decline, but ALAN has also direct effects. More than 90% of amphibians are nocturnal and their eyes are very sensitive to light. If blinded, the eyes of some frog species need more than one hour to completely readjust to darkness (Schroer and Hölker 2016).

However, lit spots might be attractive to some amphibians. Komine et al. (2020) showed that food intake in cane toads (*Rhinella marina*) was increased next to lit spots in a naturally dark area, but this effect was reduced if ambient light levels were high, e.g. due to urban ALAN or moonlight. In the common toad (*Bufo bufo*), ALAN reduced activity, while energy expenditure remained unchanged, showing a reallocation between activity and maintenance and suggesting higher stress levels (Touzot et al. 2019).

ALAN also interferes with reproduction and development. It has been shown to alter the mating times of seasonal frogs (Dias et al. 2019), change partner choice (Rand et al. 1997; Touzot et al. 2020), and reduce fertilisation rate (Touzot et al. 2020). In American toads (*Anaxyrus americanus*), ALAN decreased metamorphic duration and juvenile growth (Dananay and Benard 2018).

So far, there are only few studies on amphibians, but they do show clear negative impacts of ALAN. More research is needed on amphibians, however, this endangered group will most likely also profit from naturally dark nightscapes.

Non-flying Mammals

The Wadden Sea is habitat for several marine mammal species, for small mammals in the coastal areas, and for bats. Little is known about the impact of ALAN on marine mammals, and the few studies on seals will be discussed below.

Many small mammals adapt their activity patterns to the moon phases to reduce the risk of predation. It has been shown for several mouse species, that street light reduces nocturnal activity (Le Tallec et al. 2013; Spoelstra et al. 2015; Hoffmann et al. 2018; Hoffmann et al. 2019; Zhang et al. 2020). In mouse makis (*Microcebus murinus*), it effects the daily pattern of body temperature and the production of melatonin and testosterone (Le Tallec et al. 2013; Le Tallec et al. 2016). Changes in reproduction patterns due to ALAN have been reported in Tammar wallabies (*Macropus eugenii*) (Robert et al. 2015).

Seasonal patterns like reproduction are based on the circadian system and its regulation through melatonin. The circadian system of mammals is most sensitive to blue light at a wavelength of around 470 nm (Brainard et al. 2001). Though there have been many lab studies on mammals, data from the field are scarce and reliable light levels for melatonin suppression are missing, the effect of outdoor lights have been shown for mouse makis and tammar wallabies, even with the long-waved sodium light (Robert et al. 2015; Le Tallec et al. 2016).

The combination of field and lab studies on mammals suggest the importance of dark nights for natural circadian rhythms, the fundament for health and reproduction. There is also evidence from direct impacts of ALAN on mammals, as will be shown for seals in the following paragraphs.

SEALS

Harbour seals (*Phoca vitulina*) have been observed to hunt in lit areas, but it is not clear if their hunting efficiency increases with light. While Yurk et al. (2000) reported higher number in areas lit with white light than in unlit, he also noted a sensitivity to a red spotlight the researchers used.

Though there is no evidence of a celestial compass in seals or other marine mammals, harbour seals can learn to identify a lodestar down to 4.4 stellar magnitude. If seals do use stars for navigation, ALAN could interfere with this ability by outshining relevant stars (Mauck et al. 2005; Mauck et al. 2008).

Too little data are available on seals and worldwide no data exist on whales. It is possible that these visual hunters benefit from additional light similar to shorebirds, thus adding more predation pressure on fish populations. On the other hand, it is unclear if reproduction or sleep is affected or at which light levels melatonin suppression occurs. More research on this animal group is needed.

Bats

Bats are almost exclusively nocturnal, spending the days in roosts and covering long distances to feeding areas at night. All European species are protected. They suffer from loss of roosts, habitat fragmentation, and most likely decreased insect abundance. The considerable impact of ALAN on bat biology has been shown in several studies.

HUNTING AND COMMUTING BEHAVIOUR

ALAN influences hunting activity in several bat species. While fast-flying bats like pipistrelles and noctules show increased hunting activity around streetlights, slow-flying bats are rare or even absent from areas with illumination. The reasons are not clear yet, but while light-attraction is mostly explained by prey abundance, light aversion might be caused by increased predator risk or glare (Kuijper et al. 2008; Stone et al. 2012; Mathews et al. 2015; Spoelstra et al. 2017; Linley 2017; Azam et al. 2018; Russo et al. 2019). Indeed, light tolerant species are more active around metal halide lights than around sodium lights or LED, which correlates with the insect attraction of these light sources (Stone et al. 2015; Lewanzik and Voigt 2017; Straka et al. 2019; Haddock et al. 2019). On the other hand, red light seems to be better tolerated by light-sensitive species (Spoelstra et al. 2017; Zeale et al. 2018; Voigt et al. 2019).

However, light tolerance relates primarily to hunting behaviour. When commuting, most species prefer darker areas (Mathews et al. 2015; Hale et al. 2015; Zeale et al. 2016). The influence of streetlight on bat activity has been detected up to a distance of 50 m (Azam et al. 2018). Illuminated streets or gaps in hedges can become a barrier, resulting in fragmentation of habitats and populations (Stone et al. 2012; Azam et al. 2018). A general influence on the flying behaviour of bats has been found within a distance of up to one kilometre to the light source. Tree coverage can reduce this influence by shielding bats and providing dark passages (Straka et al. 2019).

MIGRATING BATS

On their migration along the North Sea coast and offshore, bats approach wind turbines, offshore platforms, and other structures for unknown reasons, risking collisions with these structures. It is unknown how many of these collisions happen each year, though numbers are probably considerably lower than for birds (Ballasus and Hill 2009; Hüppop and Hill 2016). It has been shown in the Baltic Sea that Nathusius' bats (*Pipistrellus nathusii*), the most common bat species in the southern North Sea, is attracted by green and red lights on poles in 100 m distance from the coast. Since migrating bats do not seem to consume much food, it is possible that the light itself attracts the bats and maybe even lures bats from the coast, resulting in energy-consuming detours and increasing the risk of collisions with man-made structures (Voigt et al. 2017; Voigt et al. 2018b).

ROOST CHOICE

Artificial light can also influence the use of roosts. A 20-year study on bat roosts in Swedish churches showed that bats were present in only few illuminated churches and roosts were often abandoned after façade illumination was installed (Rydell et al. 2017). Nocturnal light decreases flight activity of bats inside and around churches even for light-tolerant species and delays the emergence of bats from their roost (Boldogh et al. 2007; Zeale et al. 2016). Growth of juveniles can be reduced as a result (Boldogh et al. 2007). In one extreme case, the largest known Geoffroy's bat *Myotis emarginatus* colony consisting of more than 1000 individuals was abandoned (Boldogh et al. 2007).

Though in some bat species hunting success is most likely increased by ALAN it is unclear if these positive aspects outweigh the negative effects on roost availability and habitat fragmentation. In any case, ALAN changes the species composition, with light-sensitive species being rare in brighter areas (Rowse et al. 2016; Kerbiriou et al. 2020). Since bats commute over long distances, they need a network of dark corridors to connect roosts with feeding areas (Voigt et al. 2018a).

Terrestrial plants

As in marine ecosystems, terrestrial plants are the primary producers of biomass in a food web that leads to mammals and birds as top-level predators, including humans. Negative effects on plants will ultimately affect the entire ecosystem. Though there is a close link between plant physiology and light, surprisingly little research has covered the effect of outdoor ALAN on plants. The most obvious effect can be seen during spring and autumn. Changes in daylength trigger the production of buds in spring and leaf fall in autumn. Trees in direct proximity of streetlights or in generally brighter areas develop buds earlier, while shedding their leaves later. This makes them more vulnerable to frost damage (Matzke 1936; French-Constant et al. 2016; Massetti 2018).

Changes in daylength also influence the production of flowers. In the African fore-dune plant *Traganum moquinii* ALAN from promenade flood lights inhibits flowering (Viera-Pérez et al. 2019). Similar observations have been made in soy plants (Palmer et al. 2017) and big trefoil (*Lotus pedunculatus*) (Bennie et al. 2015). ALAN can also increase the toughness of leaves as shown in the smooth brome (*Bromus inermis*), making it a less suitable food species for caterpillars (Grenis and Murphy 2019).

Plants are able to use ALAN to extend photosynthesis into the night and increase biomass production (Speißer et al. 2021). However, this can damage the photosynthesis apparatus, reduce starch production, and eventually cause premature leaf death (Kwak et al. 2018). Also, ALAN can reduce the ability to regenerate from UV-damage (Vollsnies et al. 2009). It appears that the ability to use ALAN for synthesis or the amount of damage caused by it, differs between plant species.

About 85 % of plants rely on pollinators, most of them insects. ALAN can draw pollinators from the plants to artificial light sources, reducing pollination and reproduction success (Macgregor et al. 2017; Knop et al. 2017), which reduces food resources for herbivores, causing bottom-up effects in all ecosystems and change biomass production (Bennie et al. 2015).

So far, only few studies have looked into the effect of ALAN on plants. Effects on plants are usually even less considered in light planning than effects on animals. However, it is obvious that ALAN interferes directly with plant physiology and reproduction by changing biological rhythms and photosynthesis, which will reduce plant fitness. This diminishes their role in



physical and geomorphological processes. For example, plants play an essential role in the formation of the dune system by trapping sand. They also participate in micro-climate processes by cooling down the area around them.

Figure 9: Berlin city tree with streetlight in late November. Leaves directly in the light beam are still green while leaves mostly shielded from the light are already brown. Photo Annette Krop-Benesch

7. Outlook



The need to protect our nightscapes

There is growing evidence that ALAN impacts organisms and ecosystems. While some species seem to benefit directly from these effects, evidence is growing that a vast group of organisms experience negative aspects. In any case, ALAN alters biological rhythms that have been unchanged since the beginning of life, influencing organisms, populations, and ecosystems on every level. These changes are undesired, especially since the long-term consequences are unknown. In addition, ALAN can be harmful on its own, yet in combination with other environmental stressors it is expected to multiply the pressure on our ecosystems (Gaston et al. 2014; Bolton et al. 2017; Walker et al. 2019).

While the establishment of nature reserves is a vital part of conservation, in most cases the characteristics and needs of an area are only considered during daytime. Nocturnal qualities are often overlooked thus ignoring 50 % of the organisms' lifetime.

The Wadden Sea is the largest tidal flat system in the world and over wide parts of it natural processes are basically undisturbed. They follow a complex set of rhythms defined by light changes and tidal movements. The Wadden Sea is, however, under pressure due to climate change, water pollution, invasive species, and other environmental and anthropogenic stressors.

The preservation of natural darkness is vital for the function of this unique ecosystem and can strengthen its resilience to withstand other stressors. In contrast to global problems like climate change which needs a combined global effort to achieve measurable results, mitigation of ALAN can provide results on local scale within a short time.

Statements such as the La Palma Declaration 2009 or the IAU/UNOOSA Report on Dark and Quiet Skies 2020 press the urgency of nightscape conservation, not only for ecological, but also for cultural reasons (UNESCO et al. 2009; IAU/UNOOSA 2020). To achieve this goal, UNESCO and IUCN classify Dark Sky Places, the International Dark Sky Association (IDA) and the Starlight Foundation certify such places.

At present, four IDA-certified Dark Sky Places are located in the Wadden Sea World Heritage: Boschplaat and Lauwersmeer in The Netherlands and Spiekeroog and Pellworm in Germany. Other areas, including Mando in Denmark, are working towards their own certification. However, considering the reach of light emission, the size of these areas, and the distance between them, this is not enough to preserve the Wadden Sea nightscape. There is urgent need for a network of naturally dark places and corridors to allow interactions between populations, commuting and migration (Challéat et al. 2021). Considering the distances covered by migratory birds, bats, and fish, a Dark Sky Reserve covering the entire Wadden Sea World Heritage would be an invaluable conservation achievement. Without protection of the nightscape, conservation efforts cannot be totally successful.

Broader applications

A reduction of light emissions has many more positive aspects. A vast amount of light is wasted because it is not directed to the needed area (i.e., street or workspace) but into sky or landscape. In addition, light levels used often exceed actual needs. Reduction of such light waste would reduce energy consumption without disadvantages for the users.



Indeed, they might result in a better overall lighting design, because light spill can also diminish well-being of humans. Light spill into living spaces, especially into bedrooms is frequently subject of complaints (Meier 2019). ALAN has been linked to elevated rates of some hormonal cancers, obesity, depression and disruption of sleep (for review see Svechkina et al. 2020; Schröter-Schlaack et al. 2020). Residents and the visitors of health resorts would therefore benefit from naturally dark nights with well-planned lighting.

Natural darkness is also a tourism factor. People show growing interest in astro-tourism, especially if they can experience it at a destination with more tourist attractions. With reduced ALAN, the Wadden Sea area could offer tourists not only stunning wildlife, but also the attraction of a natural starry sky.

Outdoor lighting is often justified with the idea of increased safety. Though some studies reported some positive effect of light, a generalised claim cannot be confirmed (Welsh and Farrington 2008; Beyer and Ker 2009; Steinbach et al. 2015; Fotios and Gibbons 2018). There is little scientific evidence for recommended light levels (Fotios and Gibbons 2018). On the contrary, glare can cause visual constraints which can cause accidents in traffic or on ships. The installation of street, security, and work lights should therefore balance the actual benefit with the negative impact on nature and humans, especially in the proximity of water.

Actions needed

Nocturnal ecology has been overlooked until recently and still many questions need to be answered. One of the biggest questions are light thresholds. These differ between species, but some studies showed impacts of ALAN on moonlight level (i.e., Dacke et al. 2013; Kaniewska et al. 2015; Grubisic et al. 2019). More research is needed on the impact of ALAN on communities and how impacts are transferred between ecosystems (Hölker et al. 2021). Though some studies have looked at ALAN-induced changes in terrestrial and freshwater ecosystems, we need more research on marine ecosystems and their connections to other habitats (Sanders and Gaston 2018). Research on ALAN impact on marine mammals is entirely missing.

Despite these gaps in knowledge, there is enough evidence to consider ALAN as a serious stressor. To counteract brightening nightscapes, and following Principle 15 of the Rio Declaration, mitigation efforts are advisable in a precautionary manner (United Nations 1992; Committee on Education Research and Technology Assessment 2020). To achieve this, information exchange between scientists, conservationists, lighting industry, and other stakeholders is essential to balance the need for nocturnal illumination with its ecological consequences. The next chapter will give a brief overview of such measures.



Figure 10: Empty, but brightly illuminated seawall with beach (left) and mudflat (right). Photo Andreas Hänel.

8. Recommendations



Today's knowledge highlights the urgency to reduce ALAN. Due to the complex rhythmicity with diel, tidal, lunar, and seasonal components, it can be expected that ALAN affects most Wadden Sea species. Though there are many open questions about ALAN, it is obvious that artificial light at night is never neutral but interferes with organisms on many levels. A review of the studies also shows that no general recommendation can be given about less harmful light. Effects of different light spectra are species-specific; therefore, no spectrum can be considered environmentally friendly. The best objective is to reduce the impact of ALAN by creating an environmental friendly lighting by combining different parameters.

Light only if there is the necessity of a light. It is neither necessary nor mandatory to illuminate every street, pedestrian way, park, beach, etc. Light does not necessarily improve safety, nor is it necessary to illuminate all areas used by people. Frequently, people cherish unilluminated areas for recreation, and some areas should not be and are not frequented at night, especially in sensitive natural areas. Dark pockets can offer refuge to organisms and dark corridors are necessary to interconnect nocturnal habitats. The environmental damage of decorative, commercial, and advertising illumination should be considered very carefully before permitting such lights.

Reduced light trespass: Light should be directed only to the required area. This can be achieved by shielding of luminaires, pointing light downwards, and adequate light planning. If horizontal illumination cannot be avoided, e.g. for decorative facade illumination, Gobo screens can reduce light spill.

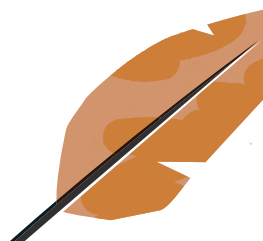
Dimming: Overlighting is a frequent source of unwanted light emissions. Lowest possible lighting levels should be used, and light levels should not exceed recommended values.

Dynamic lighting: Usage of areas can differ during the course of the night. Dimming or even switch-off during core-night hours reduces light emissions without diminishing safety. Motion-detectors can provide light on demand in rarely frequented areas. Transponders on ships and aircrafts can switch on lights when needed on offshore-structures and wind generators,

Reducing blue content: Short-waved (blue) light has been shown to have the highest negative impact (Longcore et al. 2018). Reducing this effect can be achieved by choosing a light source with a spectrum dominated by long-wavelength light or by dimming blue-rich light to a low intensity. However, even long-waved light is not without impact on organisms. Spectral composition should therefore consider local species and must be combined with other mitigation measures.



Figure 11: Illumination of a path through the dunes in the National Park. Left: Dunes without lighting. Centre: Unshielded light illuminating the dune habitat. Right: Shielding on refitted light reduces light spill, ALAN impact is further reduced by using warmwhite (2200 K) lights. Photo Andreas Hänel.



9. References



- Azam, C., Le Viol, I., Bas, Y., Zissis, G., Vernet, A., Julien, J.-F., and Kerbiriou, C. (2018). Evidence for distance and illuminance thresholds in the effects of artificial lighting on bat activity. *Landscape and Urban Planning* 175, 123–135. doi:10.1016/j.landurbplan.2018.02.011
- Ballasus, H., and Hill, K. (2009). Gefahren künstlicher Beleuchtung für ziehende Vögel und Fledermäuse. *Ber. Vogelschutz* 46, 127–157.
- Becker, A., Whitfield, A. K., Cowley, P. D., Järnegren, J., and Næsje, T. F. (2013). Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology* 50, 43–50. doi:10.1111/1365-2664.12024
- Bennie, J., Davies, T. W., Cruse, D., and Gaston, K. J. (2016). Ecological effects of artificial light at night on wild plants. *Journal of Ecology* 104, 611–620. doi:10.1111/1365-2745.12551
- Bennie, J., Davies, T. W., Cruse, D., Inger, R., and Gaston, K. J. (2018). Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *Journal of Applied Ecology* 55, 2698–2706. doi:10.1111/1365-2664.13240
- Bennie, J., Davies, T. W., Cruse, D., Inger, R., and Gaston, K. J. (2015). Cascading effects of artificial light at night: resource-mediated control of herbivores in a grassland ecosystem. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 370, 20140131-. doi:10.1098/rstb.2014.0131
- Beyer, F. R., and Ker, K. (2009). Street lighting for prevention of road traffic injuries. *Injury Prevention* 15, 282. doi:10.1136/ip.2009.022251
- Boldogh, S., Dobrosi, D., and Samu, P. (2007). The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. *Acta Chiropterologica* 9, 527–534. doi:10.3161/1733-5329(2007)9[527:TEOTIO]2.0.CO;2
- Bolliger, J., Hennet, T., Wermelinger, B., Bösch, R., Pazur, R., Blum, S., Haller, J., and Obrist, M. K. (2020). Effects of traffic-regulated street lighting on nocturnal insect abundance and bat activity. *Basic and Applied Ecology* 47, 44–56. doi:10.1016/j.baae.2020.06.003
- Bolton, D., Mayer-Pinto, M., Clark, G. F., Dafforn, K. A., Brassil, W. A., Becker, A., and Johnston, E. L. (2017). Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. *Science of the Total Environment* 576, 1–9. doi:10.1016/j.scitotenv.2016.10.037
- Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., and Pocock, M. J. O. (2021). Street lighting has detrimental impacts on local insect populations. *Science Advances* 7, eabi8322.
- Brainard, G. C., Hanifin, J. P., Greeson, J. M., Byrne, B., Glickman, G., Gerner, E., and Rollag, M. D. (2001). Action spectrum for melatonin regulation in humans: evidence for a novel circadian photoreceptor. *The Journal of neuroscience* 21, 6405–12. doi:21/16/6405 [pii]
- Brehm, G., Niermann, J., Maria, L., Nino, J., Enseling, D., Jüstel, T., Axmacher, J. A. N. C., Warrant, E., and Fiedler, K. (2021). Moths are strongly attracted to ultraviolet and blue radiation. *Insect Conservation and Diversity* 14, 188–198. doi:10.1111/icad.12476
- Van den Broeck, M., De Cock, R., Van Dongen, S., and Matthysen, E. (2021). Blinded by the light: Artificial light lowers mate attraction success in female glow-worms (*Lampyris noctiluca* l.). *Insects* 12. doi:10.3390/insects12080734
- Brüning, A., Hölker, F., Franke, S., Preuer, T., and Kloas, W. (2015). Spotlight on fish: Light pollution affects circadian rhythms of European perch but does not cause stress. *Science of the Total Environment* 511, 516–522. doi:10.1016/j.scitotenv.2014.12.094

- Brüning, A., Hölker, F., and Wolter, C. (2011). Artificial light at night: Implications for early life stages development in four temperate freshwater fish species. *Aquatic Sciences* 73, 143–152. doi:10.1007/s00027-010-0167-2
- Brüning, A., Kloas, W., Preuer, T., and Hölker, F. (2018). Influence of artificially induced light pollution on the hormone system of two common fish species, perch and roach, in a rural habitat. *Conservation Physiology* 6, 1–12. doi:10.1093/conphys/coy016
- Challéat, S., Barré, K., Laforge, A., Lapostolle, D., Franchomme, M., Sirami, C., Le Viol, I., Milian, J., and Kerbiriou, C. (2021). Grasping darkness: The dark ecological network as a social-ecological framework to limit the impacts of light pollution on biodiversity. *Ecology and Society* 26. doi:10.5751/ES-12156-260115
- Chernetsov, N. (2016). Orientation and Navigation of Migrating Birds. *Biological Bulletin* 43, 788–803. doi:10.1134/S1062359016080069
- Committee on Education Research and Technology Assessment (2020). Light pollution – extent, effects and approaches. *TAB-Fokus* 25, 1–4. Available at: <https://www.tab-beim-bundestag.de/en/pdf/publications/tab-fokus/TAB-Fokus-025.pdf>
- Coulthard, E., Norrey, J., Shortall, C., and Harris, W. E. (2019). Ecological traits predict population changes in moths. *Biological Conservation* 233, 213–219. doi:10.1016/j.biocon.2019.02.023
- Cullen, P., and McCarthy, T. K. (2000). The effects of artificial light on the distribution of catches of silver eel, *Anguilla anguilla* (L.), across the Killaloe eel weir in the Lower River Shannon. *Biology and Environment* 100, 165–169.
- Czaczkas, T. J., Bastidas-Urrutia, A. M., Ghislandi, P., and Tuní, C. (2018). Reduced light avoidance in spiders from populations in light-polluted urban environments. *The Science of Nature* 105, 64. doi:10.1007/s00114-018-1589-2
- Czarnecka, M., Kakareko, T., Jermacz, Ł., Pawlak, R., and Kobak, J. (2019). Combined effects of nocturnal exposure to artificial light and habitat complexity on fish foraging. *Science of the Total Environment* 684, 14–22. doi:10.1016/j.scitotenv.2019.05.280
- Dacke, M., Baird, E., Byrne, M., Scholtz, C. H., and Warrant, E. J. (2013). Dung beetles use the milky way for orientation. *Current Biology* 23, 298–300. doi:10.1016/j.cub.2012.12.034
- Dananay, K. L., and Benard, M. F. (2018). Artificial light at night decreases metamorphic duration and juvenile growth in a widespread amphibian. *Proceedings of the Royal Society B: Biological Sciences* 285, 1–7. doi:10.1098/rspb.2018.0367
- Davies, T. W., Bennie, J., and Gaston, K. J. (2012). Street lighting changes the composition of invertebrate communities. *Biology Letters* 8, 764–767. doi:10.1098/rsbl.2012.0216
- Davies, T. W., Bennie, J., Inger, R., and Gaston, K. J. (2013). Artificial light alters natural regimes of night-time sky brightness. *Scientific Reports* 3. doi:10.1038/srep01722
- Davies, T. W., Coleman, M., Griffith, K. M., and Jenkins, S. R. (2015). Night-time lighting alters the composition of marine epifaunal communities. *Biology Letters* 11, 20150080. doi:10.1098/rsbl.2015.0080
- Davies, T. W., Duffy, J. R., Bennie, J., and Gaston, K. J. (2014). The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment* 12, 347–355. doi:10.1890/130281
- Davies, T. W., McKee, D., Fishwick, J., Tidau, S., and Smyth, T. (2020). Biologically important artificial light at night on the seafloor. *Scientific Reports* 10, 1–10. doi:10.1038/s41598-020-69461-6
- Dias, K. S., Dosso, E. S., Hall, A. S., Schuch, A. P., and Tozetti, A. M. (2019). Ecological light pollution affects anuran calling season, daily calling period, and sensitivity to light in natural Brazilian wetlands. *Science of Nature* 106. doi:10.1007/s00114-019-1640-y

- Dominoni, D., Quetting, M., and Partecke, J. (2013). Artificial light at night advances avian reproductive physiology. *Proceedings of the Royal Society B: Biological Sciences* 280, 20123017. doi:10.1098/rspb.2012.3017
- Van Doren, B. M., Horton, K. G., Dokter, A. M., Klinck, H., Elbin, S. B., and Farnsworth, A. (2017). High-intensity urban light installation dramatically alters nocturnal bird migration. *Proceedings of the National Academy of Sciences* 114, 11175–11180. doi:10.1073/PNAS.1708574114
- Durrant, J., Botha, L. M., Green, M. P., and Jones, T. M. (2018). Artificial light at night prolongs juvenile development time in the black field cricket, *Teleogryllus commodus*. *Journal of Experimental Zoology (Mol Dev Evol)* 330, 225–233. doi:10.1002/jez.b.22810
- Dwyer, R. G., Bearhop, S., Campbell, H. A., and Bryant, D. M. (2013). Shedding light on light: Benefits of anthropogenic illumination to a nocturnally foraging shorebird. *Journal of Animal Ecology* 82, 478–485. doi:10.1111/1365-2656.12012
- Eisenbeis, G., and Eick, K. (2011). Studie zur Anziehung nachtaktiver Insekten an die Straßenbeleuchtung unter Einbeziehung von LEDs. *Natur und Landschaft* 86, 298–306.
- Elgert, C., Lehtonen, T. K., Kaitala, A., and Candolin, U. (2021). Sexual selection for bright females prevails under light pollution. *Current Zoology* 67, 329–331. doi:10.1093/cz/zoaa071
- Evans, W. R., Akashi, Y., Altman, N. S., and Manville, A. M. (2007). Response of night-migrating songbirds in cloud to colored and flashing light. *North American Birds* 60, 476–488.
- Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., Portnov, B., Rybnikova, N. A., and Furgoni, R. (2016). The New World Atlas of Artificial Night Sky Brightness. *Science Advances* June, e1600377. doi:10.1126/sciadv.1600377
- French-Constant, R. H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., and McGregor, P. K. (2016). Light pollution is associated with earlier tree budburst across the United Kingdom. *Proceedings of the Royal Society B: Biological Sciences* 283, 20160813. doi:10.1098/rspb.2016.0813
- Fleissner, G., Schuchardt, K., Neumann, D., Bali, G., Falkenberg, G., and Fleissner, G. (2008). A lunar clock changes shielding pigment transparency in larval ocelli of *Clunio marinus*. *Chronobiology International* 25, 17–30. doi:10.1080/07420520801904008
- Fobert, E. K., Burke, K., and Swearer, S. E. (2019). Artificial light at night causes reproductive failure in clownfish. *Biology Letters* 15, 20190272. doi:10.1098/rsbl.2019.0272
- Foster, J. G., Algera, D. A., Brownscombe, J. W., Zolderdo, A. J., and Cooke, S. J. (2016). Consequences of Different Types of Littoral Zone Light Pollution on the Parental Care Behaviour of a Freshwater Teleost Fish. *Water, Air, and Soil Pollution* 227. doi:10.1007/s11270-016-3106-6
- Fotios, S., and Gibbons, R. (2018). Road lighting research for drivers and pedestrians: The basis of luminance and illuminance recommendations. *Lighting Research & Technology* 50, 154–186. doi:10.1177/1477153517739055
- Fukunaga, K., Yamashina, F., Ohta, N., Mizuno, H., Takeuchi, Y., Yamauchi, C., and Takemura, A. (2019). Involvement of melatonin in transducing moon-related signals into the reproductive network of the female honeycomb grouper *Epinephelus merra*. *General and Comparative Endocrinology* 282, 113211. doi:10.1016/j.ygcen.2019.113211
- Garthe, S., and Hüppop, O. (1996). Nocturnal scavenging by gulls in the southern North Sea. *Waterbirds* 19, 232–241. doi:10.2307/1521861
- Gaston, K. J., Bennie, J., Davies, T. W., and Hopkins, J. (2013). The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biological Reviews* 88, 912–927. doi:10.1111/brv.12036

- Gaston, K. J., Davies, T. W., Nedelec, S. L., and Holt, L. A. (2017). Impacts of Artificial Light at Night on Biological Timings. *Annual Review of Ecology, Evolution, and Systematics* 48, 49–68. doi:10.1146/annurev-ecolsys-110316-022745
- Gaston, K. J., Duffy, J. P., Gaston, S., Bennie, J., and Davies, T. W. (2014). Human alteration of natural light cycles: causes and ecological consequences. *Oecologia* 176, 917–931. doi:10.1007/s00442-014-3088-2
- van Geffen, K. G., van Eck, E., de Boer, R. A., van Grunsven, R. H. A., Salis, L., Berendse, F., and Veenendaal, E. M. (2015). Artificial light at night inhibits mating in a Geometrid moth. *Insect Conservation and Diversity* 8, 282–287. doi:10.1111/icad.12116
- Van Geffen, K. G., Groot, A. T., Van Grunsven, R. H. A., Donners, M., Berendse, F., and Veenendaal, E. M. (2015). Artificial night lighting disrupts sex pheromone in a noctuid moth. *Ecological Entomology* 40, 401–408. doi:10.1111/een.12202
- Van Geffen, K. G., Van Grunsven, R. H. A., Van Ruijven, J., Berendse, F., and Veenendaal, E. M. (2014). Artificial light at night causes diapause inhibition and sex-specific life history changes in a moth. *Ecology and Evolution* 4, 2082–2089. doi:10.1002/ece3.1090
- Grenis, K., and Murphy, S. M. (2019). Direct and indirect effects of light pollution on the performance of an herbivorous insect. *Insect Science* 26, 770–776. doi:10.1111/1744-7917.12574
- Groenendijk, D., and Ellis, W. N. (2011). The state of the Dutch larger moth fauna. *Journal of Insect Conservation* 15, 95–101. doi:10.1007/s10841-010-9326-y
- Grubisic, M., Grunsven, R. H. A. Van, Kyba, C. C. M. M., Manfrin, A., and Hölker, F. (2018a). Insect declines and agroecosystems: does light pollution matter? *Annals of Applied Biology* 173, 180–189. doi:10.1111/aab.12440
- Grubisic, M., Grunsven, R. H. A. Van, Manfrin, A., Monaghan, M. T., and Franz, H. (2018b). A transition to white LED increases ecological impacts of nocturnal illumination on aquatic primary producers in a lowland agricultural drainage ditch. *Environmental Pollution* 240, 630–638. doi:10.1016/j.envpol.2018.04.146
- Grubisic, M., Haim, A., Bhusal, P., Dominoni, D. M., Gabriel, K. M. A., Jechow, A., Kupprat, F., Lerner, A., Marchant, P., Riley, W., Stebelova, K., Grunsven, R. H. A. Van, Zeman, M., Zubidat, A. E., and Hölker, F. (2019). Light Pollution, Circadian Photoreception, and Melatonin in Vertebrates. *Sustainability* 11, 1–51. doi:10.3390/su11226400
- Grunst, M. L., Raap, T., Grunst, A. S., Pinxten, R., Parenteau, C., Angelier, F., and Eens, M. (2020). Early-life exposure to artificial light at night elevates physiological stress in free-living songbirds. *Environmental Pollution* 259, 113895. doi:10.1016/j.envpol.2019.113895
- van Grunsven, R. H. A., van Deijk, J. R., Donners, M., Berendse, F., Visser, M. E., Veenendaal, E., and Spoelstra, K. (2020). Experimental light at night has a negative long-term impact on macro-moth populations. *Current Biology* 30, R694–R695. doi:10.1016/j.cub.2020.04.083
- van Grunsven, R. H. A., Donners, M., Boekee, K., Tichelaar, I., van Geffen, K. G., Groenendijk, D., Berendse, F., and Veenendaal, E. M. (2014). Spectral composition of light sources and insect phototaxis, with an evaluation of existing spectral response models. *Journal of Insect Conservation* 18, 225–231. doi:10.1007/s10841-014-9633-9
- Hadderingh, R. H., Van Aerssen, G. H. F. M., De Beijer, R. F. L. J., and Van Der Velde, G. (1999). Reaction of silver eels to artificial light sources and water currents: An experimental deflection study. *Regulated Rivers: Research & Management* 15, 365–371. doi:10.1002/(sici)1099-1646(199907/08)15:4<365::aid-rrr552>3.0.co;2-k
- Haddock, J. K., Threlfall, C. G., Law, B., and Hochuli, D. F. (2019). Responses of insectivorous bats and nocturnal insects to local changes in street light technology. *Australian Ecology* 44, 1052–1064. doi:10.1111/aec.12772
- Hale, J. D., Fairbrass, A. J., Matthews, T. J., Davies, G., and Sadler, J. P. (2015). The ecological impact of city lighting scenarios: Exploring gap crossing thresholds for urban bats. *Global Change Biology* 21, 2467–2478. doi:10.1111/gcb.12884

- Haller, J., Obrist, M., Wermelinger, B., Blum, S., and Bolliger, J. (2021). Einflüsse von Lichtfarben und Leuchtenformen auf nachtaktive Insekten und Fledermäuse. In 'LICHT 2021: Tagungsband zum 24. Europäischen Lichtkongress'. Deutsche Lichttechnische Gesellschaft e.V.
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hören, T., Goulson, D., and de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *Plos One* 12, e0185809. doi:10.1371/journal.pone.0185809
- Hallmann, C. A., Zeegers, T., Klink, R. V. A. N., Vermeulen, R., Wielink, P. V. A. N., Spijkers, H., Deijk, J. V. A. N., and Teenis, W. V. A. N. S. (2019). Declining abundance of beetles, moths and caddisflies in the Netherlands. *Insect Conservation and Diversity*. doi:10.1111/icad.12377
- Hammerschlag, N., Meyer, C. G., Grace, M. S., Kessel, S. T., Sutton, T. T., Harvey, E. S., Paris-Limouzy, C. B., Kerstetter, D. W., and Cooke, S. J. (2017). Shining a light on fish at night: An overview of fish and fisheries in the dark of night, and in deep and polar seas. *Bulletin of Marine Science* 93, 253–284. doi:10.5343/bms.2016.1082
- Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503, 163–170. doi:10.1023/B:HYDR.0000008476.23617.b0
- Hoffmann, J., Palme, R., and Eccard, J. A. (2018). Long-term dim light during nighttime changes activity patterns and space use in experimental small mammal populations. *Environmental Pollution* 238, 844–851. doi:10.1016/j.envpol.2018.03.107
- Hoffmann, J., Schirmer, A., and Eccard, J. A. (2019). Light pollution affects space use and interaction of two small mammal species irrespective of personality. *BMC Ecology* 19, 1–11. doi:10.1186/s12898-019-0241-0
- Hölker, F., Bolliger, J., Davies, T. W., Giavi, S., Jechow, A., Kalinkat, G., Longcore, T., Spoelstra, K., Tidau, S., Visser, M. E., and Knop, E. (2021). 11 Pressing Research Questions on How Light Pollution Affects Biodiversity. *Frontiers in Ecology and Evolution* 9, 1–13. doi:10.3389/fevo.2021.767177
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., and Voigt, C. C. (2010a). The Dark Side of Light: A Transdisciplinary Research Agenda for Light. *Ecology and Society* 15, 13. doi:10.1890/080129
- Hölker, F., Wolter, C., Perkin, E. K., and Tockner, K. (2010b). Light pollution as a biodiversity threat. *Trends in Ecology and Evolution* 25, 681–682. doi:10.1016/j.tree.2010.09.007
- Hölker, F., Wurzbacher, C., Weissenborn, C., Monaghan, M. T., Holzhauer, S. I. J., and Premke, K. (2015). Microbial diversity and community respiration in freshwater sediments influenced by artificial light at night. *Philosophical Transactions of the Royal Society B-Biological Sciences* 370, 20140130. doi:10.1098/rstb.2014.0130
- Horton, K. G., Nilsson, C., Van Doren, B. M., La Sorte, F. A., Dokter, A. M., and Farnsworth, A. (2019). Bright lights in the big cities: migratory birds' exposure to artificial light. *Frontiers in Ecology and the Environment* 17, 209–214. doi:10.1002/fee.2029
- Huemer, P., Kühtreiber, H., and Tarmann, G. (2010). Anlockwirkung moderner Leuchtmittel auf nachtaktive Insekten: Ergebnisse einer Feldstudie in Tirol. *Tiroler Landesumweltanwaltschaft; Tiroler Landesmuseen Betriebsgesellschaft m.b.H.*, 33 p.
- Hüppop, O., Dierschke, J., Exo, K. K.-M., Fredrich, E., and Hill, R. (2006). Bird migration studies and potential collision risk with offshore wind turbines. *Ibis* 148, 90–109. doi:10.1111/j.1474-919X.2006.00536.x
- Hüppop, O., and Hill, R. (2016). Migration phenology and behaviour of bats at a research platform in the south-eastern North Sea. *Lutra* 59, 5–22.

Hüppop, O., Michalik, B., Bach, L., Hill, R., and Pelletier, S. K. (2019). Migratory birds and bats. In 'Wildlife and Wind Farms, Conflicts and Solutions: offshore potential impact. Volume 3: Offshore: Potential Effects'. (Ed M. R. Perrow.) pp. 39–43. (Pelagic Publishing.)

IAU/UNOOSA (2020). Dark and Quiet Skies for Science and Society. Available at: <https://www.unoosa.org/documents/pdf/psa/activities/2020/DarkQuietSkies2020/Day4-Allpresentations.pdf>

IDA (2021). International Dark-Sky Association. Available at: www.darksky.org

Ineichen, S., and Rüttimann, B. (2012). Impact of artificial light on the distribution of the common European glow-worm, *Lampyris noctiluca* (Coleoptera: Lampyridae). *Lampyrid* 2, 31–36.

IUCN (2021a). IUCN motion 084 - Taking action to reduce light pollution. Available at: <https://www.iucncongress2020.org/motion/084>

IUCN (2021b). IUCN SSC Amphibian Specialist Group. Available at: <https://www.iucn-amphibians.org/>

Justice, M. J., and Justice, T. C. (2016). Attraction of Insects to Incandescent, Compact Fluorescent, Halogen, and Led Lamps in a Light Trap: Implications for Light Pollution and Urban Ecologies. *Entomological News* 125, 315–326. doi:10.3157/021.125.0502

Kaniewska, P., Alon, S., Karako-Lampert, S., Hoegh-Guldberg, O., and Levy, O. (2015). Signaling cascades and the importance of moonlight in coral broadcast mass spawning. *eLife* 4, e0999. doi:10.7554/eLife.09991.001

Kempenaers, B., Borgström, P., Loës, P., Schlicht, E., Valcu, M., Loe, P., Kempenaers, B., Borgstro, P., Schlicht, E., Valcu, M., Borgström, P., Loës, P., Schlicht, E., and Valcu, M. (2010). Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology* 20, 1735–1739. doi:10.1016/j.cub.2010.08.028

Kerbioui, C., Barré, K., Mariton, L., Pauwels, J., Zissis, G., Robert, A., and Le Viol, I. (2020). Switching LPS to LED streetlight may dramatically reduce activity and foraging of bats. *Diversity* 12, 1–14. doi:10.3390/D12040165

Kernbach, M. E., Cassone, V. M., Unnasch, T. R., and Martin, L. B. (2020). Broad-spectrum light pollution suppresses melatonin and increases West Nile virus-induced mortality in House Sparrows (*Passer domesticus*). *The Condor* 122, 1–13. doi:10.1093/condor/duaa018

Kernbach, M. E., Newhouse, D. J., Miller, J. M., Hall, R. J., Gibbons, J., Oberstaller, J., Selechnik, D., Jiang, R. H. Y., Unnasch, T. R., Balakrishnan, C. N., and Martin, L. B. (2019). Light pollution increases West Nile virus competence of a ubiquitous passerine reservoir species. *Proceedings of the Royal Society B: Biological Sciences* 286, 20191051. doi:10.1098/rspb.2019.1051

Kleijn, D., Bink, R. J., Braak, C. J. F., Van Grunsven, R., Ozinga, W. A., Roessink, I., Scheper, J. A., Schmidt, A. M., WallisdeVries, M. F., Wegman, R., Van der Zee, F. F., and Zeegers, T. (2018). Achteruitgang insectenpopulaties in Nederland: trends, oorzaken en kennislacunes. 90 p.

Kleinteich, A., and Schneider, J. M. (2011). Developmental strategies in an invasive spider: constraints and plasticity. *Ecological Entomology* 36, 82–93. doi:10.1111/j.1365-2311.2010.01249.x

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., and Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature* 548, 206–209. doi:10.1038/nature23288

Koen, E. L., Minnaar, C., Roever, C. L., and Boyles, J. G. (2018). Emerging threat of the 21st century lightscape to global biodiversity. *Global Change Biology* 24, 0–1. doi:10.1111/gcb.14146

Komine, H., Koike, S., and Schwarzkopf, L. (2020). Impacts of artificial light on food intake in invasive toads. *Scientific Reports* 10, 3–5. doi:10.1038/s41598-020-63503-9

- Kuijper, D. P. J., Schut, J., Dullemen, D. Van, Toorman, H., Goossens, N., Ouwehand, J., and Limpens, J. G. A. (2008). Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*). *Lutra* 51, 37–49. doi:2
- Kupprat, F., Hölker, F., and Kloas, W. (2020). Can skyglow reduce nocturnal melatonin concentrations in Eurasian perch? *Environmental Pollution* 262, 114324. doi:10.1016/j.envpol.2020.114324
- Kurvers, R. H. J. M., Drägestein, J., Hölker, F., Jechow, A., Krause, J., and Bierbach, D. (2018). Artificial Light at Night Affects Emergence from a Refuge and Space Use in Guppies. *Scientific Reports* 8, 14131. doi:10.1038/s41598-018-32466-3
- Kwak, M., Je, S., Cheng, H., Seo, S., Park, J., Baek, S., Khaine, I., Lee, T., Jang, J., Li, Y., Kim, H., Lee, J., Kim, J., and Woo, S. (2018). Night Light-Adaptation Strategies for Photosynthetic Apparatus in Yellow-Poplar (*Liriodendron tulipifera* L.) Exposed to Artificial Night Lighting. *Forests* 9, 74. doi:10.3390/f9020074
- Kyba, C. C. M., and Hölker, F. (2013). Do artificially illuminated skies affect biodiversity in nocturnal landscapes? *Landscape Ecology* 28, 1637–1640. doi:10.1007/s10980-013-9936-3
- Kyba, C. C. M., Kuester, T., De Miguel, A. S., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C. D., Gaston, K. J., and Guanter, L. (2017). Artificially lit surface of Earth at night increasing in radiance and extent - Supplementary Materials. *Science Advances* 3. doi:10.1126/sciadv.1701528
- Kyba, C. C. M., Ruhtz, T., Fischer, J., and Hölker, F. (2011). Lunar skylight polarization signal polluted by urban lighting. *Journal of Geophysical Research Atmospheres* 116, 1–6. doi:10.1029/2011JD016698
- Langevelde, F. Van, Braamburg-annegarn, M., Huigens, M. E., Deijk, R. Van, Ellis, W. N., Groendijk, R., Poitevin, O., Grunsvan, R. H. A. Van, Vos, R. De, Vos, R. A., Franz, M., and Wallisdevries, M. F. (2018). Declines in moth populations stress the need for conserving dark nights. *Global Change Biology* 24, 925–932. doi:10.1111/gcb.14008
- van Langevelde, F., van Grunsvan, R. H. A., Veenendaal, E. M., and Fijen, T. P. M. (2017). Artificial night lighting inhibits feeding in moths. *Biology Letters* 13, 20160874. doi:10.1098/rsbl.2016.0874
- Levy, K., Wegrzyn, Y., Efronny, R., Barnea, A., and Ayali, A. (2021). Lifelong exposure to artificial light at night impacts stridulation and locomotion activity patterns in the cricket *Gryllus bimaculatus*. *Proceedings of the Royal Society B: Biological Sciences* 288, 20211626. doi:10.1098/rspb.2021.1626
- Lewanzik, D., and Voigt, C. C. (2017). Transition from conventional to light-emitting diode street lighting changes activity of urban bats. *Journal of Applied Ecology* 54, 264–271. doi:10.1111/1365-2664.12758
- Lewis, S. M., Wong, C. H. A. Y., Owens, A. C. S., Fallon, C., and Jepsen, S. (2020). A Global Perspective on Firefly Extinction Threats. *BioScience* 70, 157–167. doi:10.1093/biosci/biz157
- Linley, G. D. (2017). The impact of artificial lighting on bats along native coastal vegetation. *Australian Mammalogy* 39, 178–184. doi:10.1071/AM15047
- Longcore, T., Aldern, H. L., Eggers, J. F., Flores, S., Franco, L., Hirshfield-Yamanishi, E., Petrinc, L. N., Yan, W. A., and Barroso, A. M. (2015). Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. *Philosophical Transactions of the Royal Society: Biological Sciences* 370, 20140125. doi:10.1098/rstb.2014.0125
- Longcore, T., Rich, C., Mineau, P., MacDonald, B., Bert, D. G., Sullivan, L. M., Mutrie, E., Gauthreaux, S. A., Avery, M. L., Crawford, R. L., Manville, A. M., Travis, E. R., and Drake, D. (2012). An Estimate of Avian Mortality at Communication Towers in the United States and Canada. *PLoS ONE* 7, e34025. doi:10.1016/j.biocon.2012.09.019

- Longcore, T., Rich, C., Mineau, P., MacDonald, B., Bert, D. G., Sullivan, L. M., Mutrie, E., Gauthreaux, S. A., Avery, M. L., Crawford, R. L., Manville, A. M., Travis, E. R., and Drake, D. (2013). Avian mortality at communication towers in the United States and Canada: Which species, how many, and where? *Biological Conservation* 158, 410–419. doi:10.1016/j.biocon.2012.09.019
- Longcore, T., Rodríguez, A., Witherington, B., Penniman, J. F., Herf, L., and Herf, M. (2018). Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 329, 511–521. doi:10.1002/jez.2184
- Loss, S. R., Lao, S., Eckles, J. W., Anderson, A. W., Blair, R. B., and Turner, R. J. (2019). Factors influencing bird-building collisions in the downtown area of a major North American city. *PLoS ONE* 14, 1–24. doi:10.1371/journal.pone.0224164
- Loss, S. R., Will, T., and Marra, P.P. (2015). Direct Mortality of Birds from Anthropogenic Causes. *Annual Review of Ecology, Evolution, and Systematics* 46, 99–120. doi:10.1146/annurev-ecolsys-112414-054133
- Ludvigsen, M., Berge, J., Geoffroy, M., Cohen, J. H., De La Torre, P.R., Nornes, S. M., Singh, H., Sørensen, A. J., Daase, M., and Johnsen, G. (2018). Use of an Autonomous Surface Vehicle reveals small-scale diel vertical migrations of zooplankton and susceptibility to light pollution under low solar irradiance. *Science Advances* 4, eaap9887. doi:10.1126/sciadv.aap9887
- Macgregor, C. J., Evans, D. M., Fox, R., and Pocock, M. J. O. (2017). The dark side of street lighting: impacts on moths and evidence for the disruption of nocturnal pollen transport. *Global Change Biology* 23, 697–707. doi:10.1111/gcb.13371
- Maggi, E., and Benedetti-Cecchi, L. (2018). Trophic compensation stabilizes marine primary producers exposed to artificial light at night. *Marine Ecology Progress Series* 606, 1–5. doi:10.3354/meps12769
- Maggi, E., Bongiorno, L., Fontanini, D., Capocchi, A., Dal Bello, M., Giacomelli, A., and Benedetti-Cecchi, L. (2020). Artificial light at night erases positive interactions across trophic levels. *Functional Ecology* 34, 694–706. doi:10.1111/1365-2435.13485
- Mammola, S., Isaia, M., Demonte, D., Triolo, P., and Nervo, M. (2018). Artificial lighting triggers the presence of urban spiders and their webs on historical buildings. *Landscape and Urban Planning* 180, 187–194. doi:10.1016/j.landurbplan.2018.09.003
- Manfrin, A., Singer, G., Larsen, S., Weiß, N., van Grunsven, R. H. A., Weiß, N.-S., Wohlfahrt, S., Monaghan, M. T., and Hölker, F. (2017). Artificial Light at Night Affects Organism Flux across Ecosystem Boundaries and Drives Community Structure in the Recipient Ecosystem. *Frontiers in Environmental Science* 5, 61. doi:10.3389/fenvs.2017.00061
- Marczak, L. B., and Richardson, A. E. J. S. (2008). Growth and development rates in a riparian spider are altered by asynchrony between the timing and amount of a resource subsidy. *Oecologia* 156, 249–258. doi:10.1007/s00442-008-0989-y
- Martín, B., Pérez, H., and Ferrer, M. (2021). Light - Emitting Diodes (LED): A Promising Street Light System to Reduce the Attraction to Light of Insects. *Diversity* 13, 89.
- Massetti, L. (2018). Assessing the impact of street lighting on *Platanus x acerifolia* phenology. *Urban Forestry & Urban Greening* 34, 71–77. doi:10.1016/j.ufug.2018.05.015
- Mathews, F., Roche, N., Aughney, T., Jones, N., Day, J., Baker, J., and Langton, S. (2015). Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. *Philosophical Transactions of the Royal Society B* 370, 20140124. doi:10.1098/rstb.2014.0124
- Matzke, E. B. (1936). The Effect of Street Lights in Delaying Leaf-Fall in Certain Trees. *American Journal of Botany* 23, 446–452.
- Mauck, B., Brown, D., Schlosser, W., Schaeffel, F., and Dehnhardt, G. (2005). How a harbor seal sees the night sky. *Marine Mammal Science* 21, 646–656. doi:10.1111/j.1748-7692.2005.tb01257.x

- Mauck, B., Gläser, N., Schlosser, W., and Dehnhardt, G. (2008). Harbour seals (*Phoca vitulina*) can steer by the stars. *Animal Cognition* 11, 715–718. doi:10.1007/s10071-008-0156-1
- McLaren, J. D., Buler, J. J., Schreckengost, T., Smolinsky, J. A., Boone, M., Emiel van Loon, E., Dawson, D. K., and Walters, E. L. (2018). Artificial light at night confounds broad-scale habitat use by migrating birds. *Ecology Letters* 21, 356–364. doi:10.1111/ele.12902
- McMunn, M. S., Yang, L. H., Ansalmo, A., Bucknam, K., Claret, M., Clay, C., Cox, K., Dungey, D. R., Jones, A., Kim, A. Y., Kubacki, R., Le, R., Martinez, D., Reynolds, B., Schroder, J., Wood, E., and Schmidt, J. (2019). Artificial Light Increases Local Predator Abundance, Predation Rates, and Herbivory. *Environmental Entomology* 48, 1331–1339. doi:10.1093/ee/nvz103
- Mehner, T. (2012). Diel vertical migration of freshwater fishes - proximate triggers, ultimate causes and research perspectives. *Freshwater Biology* 57, 1342–1359. doi:10.1111/j.1365-2427.2012.02811.x
- Meier, J. M. (2019). Contentious Light: An Analytical Framework for Lighting Conflicts. *International Journal of Sustainable Lighting* 20, 62–77. doi:10.26607/ijsl.v20i2.89
- Moore, M., Pierce, S., Walsh, H., Kvalvik, S., and Lim, J. (2000). Urban light pollution alters the diel vertical migration of *Daphnia*. *Internationale Vereinigung für Theoretische und Angewandte Limnologie Verhandlungen* 27, 779–782. doi:10.1002/9780470694961.ch1
- Muheim, R., Sjöberg, S., and Pinzon-Rodriguez, A. (2016). Polarized light modulates light-dependent magnetic compass orientation in birds. *Proceedings of the National Academy of Sciences* 113, 1654–1659. doi:10.1073/pnas.1513391113
- Navarro-Barranco, C., and Hughes, L. E. (2015). Effects of light pollution on the emergent fauna of shallow marine ecosystems: Amphipods as a case study. *Marine Pollution Bulletin* 94, 235–240. doi:10.1016/j.marpolbul.2015.02.023
- Neilson, J. D., and Perry, R. I. (1990). Diel vertical migrations of juvenile fish: an obligate or facultative process? *Advances in Marine Biology* 26: 115-168.
- Ouyang, J. Q., Davies, S., and Dominoni, D. (2018). Hormonally mediated effects of artificial light at night on behavior and fitness: Linking endocrine mechanisms with function. *Journal of Experimental Biology* 221. doi:10.1242/jeb.156893
- Ouyang, J. Q., de Jong, M., van Grunsven, R. H. A., Matson, K. D., Haussmann, M. F., Meerlo, P., Visser, M. E., and Spoelstra, K. (2017). Restless roosts: Light pollution affects behavior, sleep, and physiology in a free-living songbird. *Global Change Biology* 23, 4987–4994. doi:10.1111/gcb.13756
- Ouyang, J. Q., De Jong, M., Hau, M., Visser, M. E., Van Grunsven, R. H. A., and Spoelstra, K. (2015). Stressful colours: Corticosterone concentrations in a free-living songbird vary with the spectral composition of experimental illumination. *Biology Letters* 11. doi:10.1098/rsbl.2015.0517
- Palmer, M., Gibbons, R., Bhagavathula, R., Holshouser, D., and Davidson, D. (2017). Roadway Lighting's impact on altering soybean growth: Volume 1. Available at: <https://apps.ict.illinois.edu/projects/getfile.asp?id=5252>
- Parkinson, E., Lawson, J., and Tiegs, S. D. (2020). Artificial light at night at the terrestrial-aquatic interface: Effects on predators and fluxes of insect prey. *PLoS ONE* 15, 1–14. doi:10.1371/journal.pone.0240138
- Pawson, S. M., and Bader, M. K. F. (2014). LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications* 24, 1561–1568. doi:10.1890/14-0468.1
- Pendoley, K., Bell, C., Surman, C., Choi, J., Rodriguez, A., Chiaradia, A., Bridger, G., Carey, A., Mitchell, A., and Wilson, P. (2020). National Light Pollution Guidelines for Wildlife Including Marine Turtles, Seabirds and Migratory Shorebirds. Available at: <https://www.environment.gov.au/biodiversity/publications/national-light-pollution-guidelines-wildlife>

- Poot, H., Ens, B. J., Vries, H. De, Donners, M. a H., Wernand, M. R., and Marquenie, J. M. (2009). Green Light for Nocturnally Migrating Birds. *Ecology and Society* 13, 47. doi:1
- Pulgar, J., Zeballos, D., Vargas, J., Aldana, M., Manriquez, P., Manriquez, K., Quijón, P. A., Widdicombe, S., Anguita, C., Quintanilla, D., and Duarte, C. (2019). Endogenous cycles, activity patterns and energy expenditure of an intertidal fish is modified by artificial light pollution at night (ALAN). *Environmental Pollution* 244, 361–366. doi:10.1016/j.envpol.2018.10.063
- Raap, T., Casasole, G., Pinxten, R., and Eens, M. (2016a). Early life exposure to artificial light at night affects the physiological condition: An experimental study on the ecophysiology of free-living nestling songbirds. *Environmental Pollution* 218, 909–914. doi:10.1016/j.envpol.2016.08.024
- Raap, T., Pinxten, R., and Eens, M. (2018). Artificial light at night causes an unexpected increase in oxalate in developing male songbirds. *Conservation Physiology* 6, 1–7. doi:10.1093/conphys/coy005
- Raap, T., Pinxten, R., and Eens, M. (2016b). Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environmental Pollution* 215, 125–134. doi:10.1016/j.envpol.2016.04.100
- Raible, F., Takekata, H., and Tessmar-Raible, K. (2017). An Overview of Monthly Rhythms and Clocks. *Frontiers in Neurology* 8, 189. doi:10.3389/fneur.2017.00189
- Rand, A. S., Bridarolli, M. E., Dries, L., and Ryan, M. J. (1997). Light levels influence female choice in Tungara frogs: Predation risk assessment? *Copeia*, 447–450. doi:10.2307/1447770
- Rebke, M., Dierschke, V., Weiner, C. N., Aumüller, R., Hill, K., and Hill, R. (2019). Attraction of nocturnally migrating birds to artificial light: The influence of colour, intensity and blinking mode under different cloud cover conditions. *Biological Conservation* 233, 220–227. doi:10.1016/j.biocon.2019.02.029
- Robert, K. A., Lesku, J. A., Partecke, J., and Chambers, B. (2015). Artificial light at night desynchronizes strictly seasonal reproduction in a wild mammal. *Proceedings of the Royal Society B: Biological Sciences* 282, 20151745. doi:10.1098/rspb.2015.1745
- Rodríguez, A., Arcos, J. M., Bretagnolle, V., Dias, M. P., Holmes, N. D., and Louzao, M. (2019). Future Directions in Conservation Research on Petrels and Shearwaters. *Frontiers in Marine Science* 6, 94. doi:10.3389/fmars.2019.00094
- Rodríguez, A., Dann, P., and Chiaradia, A. (2017a). Reducing light-induced mortality of seabirds: High pressure sodium lights decrease the fatal attraction of shearwaters. *Journal for Nature Conservation* 39, 68–72. doi:10.1016/j.jnc.2017.07.001
- Rodríguez, A., Holmes, N. D., Ryan, P. G., Wilson, K. J., Faulquier, L., Murillo, Y., Raine, A. F., Penniman, J. F., Neves, V., Rodríguez, B., Negro, J. J., Chiaradia, A., Dann, P., Anderson, T., Metzger, B., Shirai, M., Deppe, L., Wheeler, J., Hodum, P., Gouveia, C., Carmo, V., Carreira, G. P., Delgado-Alburquerque, L., Guerra-Correa, C., Couzi, F. X., Travers, M., and Corre, M. Le (2017b). Seabird mortality induced by land-based artificial lights. *Conservation Biology* 31, 986–1001. doi:10.1111/cobi.12900
- Ronconi, R. A., Allard, K. A., and Taylor, P. D. (2015). Bird interactions with offshore oil and gas platforms: Review of impacts and monitoring techniques. *Journal of Environmental Management* 147, 34–45. doi:10.1016/j.jenvman.2014.07.031
- Rowse, E. G., Harris, S., and Jones, G. (2016). The switch from low-pressure sodium to light emitting diodes does not affect bat activity at street lights. *PLoS ONE* 11, 1–14. doi:10.1371/journal.pone.0150884
- Russ, A., Reitemeier, S., Weissmann, A., Gottschalk, J., Einspanier, A., and Klenke, R. (2015). Seasonal and urban effects on the endocrinology of a wild passerine. *Ecology and Evolution* 5, 5698–5710. doi:10.1002/ece3.1820

- Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P., and Ancillotto, L. (2019). Artificial illumination near rivers may alter bat-insect trophic interactions. *Environmental Pollution* 252, 1671–1677. doi:10.1016/j.envpol.2019.06.105
- Rydell, J., Eklöf, J., and Sánchez-Navarro, S. (2017). Age of enlightenment: long-term effects of outdoor aesthetic lights on bats in churches. *Royal Society Open Science* 4, 161077. doi:10.1098/rsos.161077
- Sameoto, D., Cochrane, N. A., and Herman, A. W. (1985). Response of biological acoustic backscattering to ships' lights. *Canadian Journal of Fisheries and Aquatic Sciences* 42, 1535–1543. doi:10.1139/f85-192
- Sánchez de Miguel, A., Bennie, J., Rosenfeld, E., Dzurjak, S., and Gaston, K. J. (2021). First Estimation of Global Trends in Nocturnal Power Emissions Reveals Acceleration of Light Pollution. *Remote Sensing* 13, 3311. doi:10.3390/rs13163311
- Sanders, D., Frago, E., Kehoe, R., Patterson, C., and Gaston, K. J. (2021). A meta-analysis of biological impacts of artificial light at night. *Nature Ecology & Evolution* 5, 74–81. doi:10.1038/s41559-020-01322-x
- Sanders, D., and Gaston, K. J. (2018). How ecological communities respond to artificial light at night. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 1–7. doi:10.1002/jez.2157
- Santos, C. D., Miranda, A. C., Granadeiro, J. R., Lourenço, P. M., Saraiva, S., and Palmeirim, J. M. (2010). Effects of artificial illumination on the nocturnal foraging of waders. *Acta Oecologica* 36, 166–172. doi:10.1016/j.actao.2009.11.008
- Schligler, J., Cortese, D., Beldade, R., Swearer, S. E., Mills, S. C., and Mills, S. C. (2021). Long-term exposure to artificial light at night in the wild decreases survival and growth of a coral reef fish. *Proceedings of the Royal Society B: Biological Sciences* 288: 20210454.
- Schroer, S., and Hölker, F. (2016). Impact of lighting on flora and fauna. In 'Handbook of Advanced Lighting Technology'. (Eds R. Karlicek, C.-C. Sun, G. Zissis, and R. Ma.) pp. 1–33. (Springer.) doi:10.1007/978-3-319-00176-0
- Schröter-Schlaack, C., Schulte-Römer, N., and Revermann, C. (2020). Lichtverschmutzung – Ausmaß, gesellschaftliche und ökologische Auswirkungen sowie Handlungsansätze. Available at: <https://www.tab-beim-bundestag.de/de/pdf/publikationen/berichte/TAB-Arbeitsbericht-ab186.pdf>
- Senzaki, M., Barber, J. R., Phillips, J. N., Carter, N. H., Cooper, C. B., Ditmer, M. A., Fristrup, K. M., McClure, C. J. W., Mennitt, D. J., Tyrrell, L. P., Vukomanovic, J., Wilson, A. A., and Francis, C. D. (2020). Sensory pollutants alter bird phenology and fitness across a continent. *Nature* 587, 605–609. doi:10.1038/s41586-020-2903-7
- Da Silva, A., Valcu, M., and Kempenaers, B. (2015). Light pollution alters the phenology of dawn and dusk singing in common European songbirds. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 370, 1–9. doi:10.1098/rstb.2014.0126
- Somers-Yeates, R., Hodgson, D., McGregor, P. K., Spalding, A., and French-Constant, R. H. (2013). Shedding light on moths: Shorter wavelengths attract noctuids more than geometrids. *Biology Letters* 9, 20130376. doi:10.1098/rsbl.2013.0376
- Soneira, M. (2013). Auswirkungen auf die Insekten-Fauna durch die Umrüstung von Kugelleuchten auf LED-Beleuchtungen. Auftragsstudie der Stadt Wien. Available at: <https://www.wien.gv.at/verkehr/licht/pdf/studie-insekten.pdf>
- La Sorte, F. A., Fink, D., Buler, J. J., Farnsworth, A., and Cabrera-cruz, S. A. (2017). Seasonal associations with urban light pollution for nocturnally migrating bird populations. *Global Change Biology*, 1–11. doi:10.1111/gcb.13792
- Speißer, B., Liu, Y., and van Kleunen, M. (2021). Biomass responses of widely and less-widely naturalized alien plants to artificial light at night. *Journal of Ecology* 109, 1819–1827. doi:10.1111/1365-2745.13607

- Spoelstra, K., van Grunsven, R. H. A., Donners, M., Gienapp, P., Huigens, M. E., Slaterus, R., Berendse, F., Visser, M. E., and Veenendaal, E. (2015). Experimental illumination of natural habitat - an experimental set-up to assess the direct and indirect ecological consequences of artificial light of different spectral composition. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370, 20140129. doi:10.1098/rstb.2014.0129
- Spoelstra, K., van Grunsven, R. H. A., Ramakers, J. J. C., Ferguson, K. B., Raap, T., Donners, M., Veenendaal, E. M., and Visser, M. E. (2017). Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. *Proceedings of the Royal Society of London B: Biological Sciences* 284, 11–15. doi:10.1098/rspb.2017.0075
- Steinbach, R., Perkins, C., Tompson, L., Johnson, S., Armstrong, B., Green, J., Grundy, C., Wilkinson, P., and Edwards, P. (2015). The effect of reduced street lighting on road casualties and crime in England and Wales: controlled interrupted time series analysis. *Journal of Epidemiology and Community Health* 69, 1118–1124. doi:10.1136/jech-2015-206012
- Stewart, A. J. A., Perl, C. D., and Niven, J. E. (2020). Artificial lighting impairs mate attraction in a nocturnal capital breeder. *Journal of Experimental Biology* 223. doi:10.1242/jeb.229146
- Stone, E. L., Jones, G., and Harris, S. (2012). Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. *Global Change Biology* 18, 2458–2465. doi:10.1111/j.1365-2486.2012.02705.x
- Stone, E. L., Wakefield, A., Harris, S., Jones, G., and Stone, E. L. (2015). The impacts of new street light technologies: experimentally testing the effects on bats of changing from low- pressure sodium to white metal halide. *Philosophical Transactions Royal Society B* 370, 20140127. doi:10.1098/rstb.2014.0127
- Straka, T. M., Wolf, M., Gras, P., Buchholz, S., and Voigt, C. C. (2019). Tree cover mediates the effect of artificial light on urban bats. *Frontiers in Ecology and Evolution* 7, 1–11. doi:10.3389/fevo.2019.00091
- Sullivan, S. M. P., Hossler, K., and Meyer, L. A. (2019). Artificial lighting at night alters aquatic-riparian invertebrate food webs. *Ecological Applications* 29. doi:10.1002/eap.1821
- Svechikina, A., Portnov, B. A., and Trop, T. (2020). The impact of artificial light at night on human and ecosystem health: a systematic literature review. *Landscape Ecology* 35, 1725–1742. doi:10.1007/s10980-020-01053-1
- Sweeney, A. M., Boch, C. A., Johnsen, S., and Morse, D. E. (2011). Twilight spectral dynamics and the coral reef invertebrate spawning response. *Journal of Experimental Biology* 214, 770–777. doi:10.1242/jeb.043406
- Syposz, M., Gonçalves, F., Carty, M., Hoppitt, W., and Manco, F. (2018). Factors influencing Manx Shearwater grounding on the west coast of Scotland. *Ibis* 160, 846–854. doi:10.1111/ibi.12594
- Syposz, M., Padgett, O., Willis, J., Van Doren, B. M., Gillies, N., Fayet, A. L., Wood, M. J., Alejo, A., and Guilford, T. (2021). Avoidance of different durations, colours and intensities of artificial light by adult seabirds. *Scientific Reports* 11, 1–14. doi:10.1038/s41598-021-97986-x
- Szekeres, P., Wilson, A. D. M., Haak, C. R., Danylchuk, A. J., Brownscombe, J. W., Elvidge, C. K., Shultz, A. D., Birnie-Gauvin, K., and Cooke, S. J. (2017). Does coastal light pollution alter the nocturnal behavior and blood physiology of juvenile bonefish (*Albula vulpes*)? *Bulletin of Marine Science* 93, 491–505. doi:10.5343/bms.2016.1061
- Tabor, R. A., Bell, A. T. C., Lantz, D. W., Gregersen, C. N., Berge, H. B., and Hawkins, D. K. (2017). Phototaxic behavior of subyearling salmonids in the nearshore area of two urban lakes in Western Washington state. *Transactions of the American Fisheries Society* 146, 753–761. doi:10.1080/00028487.2017.1305988

- Talanda, J., Maszczyk, P., and Babkiewicz, E. (2018). The reaction distance of a planktivorous fish (*Scardinius erythrophthalmus*) and the evasiveness of its prey (*Daphnia pulex* × *pulicaria*) under different artificial light spectra. *Limnology* 19, 311–319. doi:10.1007/s10201-018-0548-0
- Le Tallec, T., Perret, M., and Théry, M. (2013). Light pollution modifies the expression of daily rhythms and behavior patterns in a nocturnal primate. *PLoS ONE* 8, e79250. doi:10.1371/journal.pone.0079250
- Le Tallec, T., Théry, M., and Perret, M. (2016). Melatonin concentrations and timing of seasonal reproduction in male mouse lemurs (*Microcebus murinus*) exposed to light pollution. *Journal of Mammalogy* 97, 753–760. doi:10.1093/jmammal/gyw003
- Thakurdas, P., Sharma, S., Vanlalhratpuia, K., Sinam, B., Chib, M., Shivagaje, A., and Joshi, D. (2009). Light at night alters the parameters of the eclosion rhythm in a tropical fruit fly, *Drosophila jambulina*. *Chronobiology International* 26, 1575–1586.
- Thomas, J. R., James, J., Newman, R. C., Riley, W. D., Griffiths, S. W., and Cable, J. (2016). The impact of streetlights on an aquatic invasive species: Artificial light at night alters signal crayfish behaviour. *Applied Animal Behaviour Science* 176, 143–149. doi:10.1016/j.applanim.2015.11.020
- Thorson, G. (1964). Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. *Ophelia* 1, 167–208. doi:10.1080/00785326.1964.10416277
- Touzot, M., Lengagne, T., Secondi, J., Desouhant, E., Théry, M., Dumet, A., Duchamp, C., and Mondy, N. (2020). Artificial light at night alters the sexual behaviour and fertilisation success of the common toad. *Environmental Pollution* 259, 113883. doi:10.1016/j.envpol.2019.113883
- Touzot, M., Teulier, L., Lengagne, T., Secondi, J., Théry, M., Libourel, P. A., Guillard, L., and Mondy, N. (2019). Artificial light at night disturbs the activity and energy allocation of the common toad during the breeding period. *Conservation Physiology* 7. doi:10.1093/conphys/coz002
- Underwood, C. N., Davies, T. W., and Queirós, A. M. (2017). Artificial light at night alters trophic interactions of intertidal invertebrates. *Journal of Animal Ecology* 86, 781–789. doi:10.1111/1365-2656.12670
- UNESCO, Starlight Initiative, La Palma Biosphere Reserve, Instituto de Astrofísica de Canarias, Government of the Canary Islands, and Spanish Ministry of the Environment (2009). Declaration in Defense of the Night Sky and the Right to Starlight (La Palma Declaration). In 'International Conference in Defence of the Quality of the Night Sky and the Right to Observe the Stars - StarLight 2007'. pp. 14
- United Nations (1992). A/CONF.151/26/Vol.I: Rio Declaration on Environment and Development. Report of the United Nations Conference on Environment and Development I, 1–5. Available at: <http://www.un.org/documents/ga/conf151/aSaatinini.html>, orang yang dimaksud adalah bank, yaitu suatu lembaga keuangan berupa perusahaan yang mewakili nasabah untuk melakukan: [conf15126-1annex1.htm](http://www.un.org/documents/ga/conf151/aSaatinini.html)
- Viera-Pérez, M., Hernández-Calvento, L., Hesp, P. A., and Santana-del Pino, A. (2019). Artificial light on foredune plants. *Ecology* 100, e02678. doi:10.1002/ecy.2678
- Voigt, C. C., Azam, C., Dekker, J., Ferguson, J., Fritze, M., Gazaryan, S., Hölker, F., Jones, G., Leader, N., Lewanzik, D., Limpens, H. J. G. A., Mathews, F., Rydell, J., Schofield, H., Spoelstra, K., and Zagnajster, M. (2018a). Guidelines for considerations of bats in lighting projects. EUROBATS Publication Series 8, 62. Available at: https://www.eurobats.org/sites/default/files/documents/publications/publication_series/WEB_EUROBATS_08_ENGL_NVK_19092018.pdf
- Voigt, C. C., Rehnig, K., Lindecke, O., and Petersons, G. (2018b). Migratory bats are attracted by red light but not by warm-white light: Implications for the protection of nocturnal migrants. *Ecology and Evolution* 8, 9353–9361. doi:10.1002/ece3.4400
- Voigt, C. C., Roeleke, M., Marggraf, L., Petersons, G., and Voigt-Heucke, S. L. (2017). Migratory bats respond to artificial green light with positive phototaxis. *PLoS ONE* 12, 1–11. doi:10.1371/journal.pone.0177748

- Vollsnes, A. V., Eriksen, A. B., Otterholt, E., Kvaal, K., Oxaal, U., and Futsaether, C. M. (2009). Visible foliar injury and infrared imaging show that daylength affects short-term recovery after ozone stress in *Trifolium subterraneum*. *Journal of Experimental Botany* 60, 3677–3686. doi:10.1093/jxb/erp213
- Wakefield, A., Broyles, M., Stone, E. L., Harris, S., and Jones, G. (2017). Quantifying the attractiveness of broad-spectrum street lights to aerial nocturnal insects. *Journal of Applied Ecology* 55, 714–722. doi:10.1111/1365-2664.13004
- Wakefield, A., Broyles, M., Stone, E. L., Jones, G., and Harris, S. (2016). Experimentally comparing the attractiveness of domestic lights to insects: Do LEDs attract fewer insects than conventional light types? *Ecology and Evolution* 6, 8028–8036. doi:10.1002/ece3.2527
- Walker, W. H., Meléndez-Fernández, O. H., Nelson, R. J., and Reiter, R. J. (2019). Global climate change and invariable photoperiods: A mismatch that jeopardizes animal fitness. *Ecology and Evolution* 9, 10044–10054. doi:10.1002/ece3.5537
- Watanuki, Y. (2014). Moonlight Avoidance Behavior in Leach's Storm-Petrels as a Defense against Slaty-Backed Gulls. *Auk* 103, 14–22.
- Welsh, B. C., and Farrington, D. P. (2008). Effects of improved street lighting on crime: a systematic review. *Campbell Systematic Reviews*, 59. doi:10.4073/csr.2008.13
- Westby, K. M., and Medley, K. A. (2020). Cold nights, city lights: Artificial light at night reduces photoperiodically induced diapause in urban and rural populations of *Aedes albopictus* (Diptera: Culicidae). *Journal of Medical Entomology* 57, 1694–1699. doi:10.1093/jme/tjaa139
- Wilcockson, D., and Zhang, L. (2008). Circatidal clocks. *Current Biology* 18, R754. doi:10.1038/3703
- Willmott, N. J., Henneken, J., Elgar, M. A., and Jones, T. M. (2019). Guiding lights: Foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night. *Ethology* 125, 289–297. doi:10.1111/eth.12852
- Wilson, J. F., Baker, D., Cheney, J., Cook, M., Ellis, M., Freestone, R., Gardner, D., Geen, G., Hemming, R., Hodgers, D., Howarth, S., Jupp, A., Lowe, N., Orridge, S., Shaw, M., Smith, B., Turner, A., and Young, H. (2018). A role for artificial night-time lighting in long-term changes in populations of 100 widespread macro-moths in UK and Ireland: a citizen-science study. *Journal of Insect Conservation* 22, 189–196. doi:10.1007/s10841-018-0052-1
- Yurk, H., and Trites, A. W. (2000). Experimental Attempts to Reduce Predation by Harbor Seals on Out-Migrating Juvenile Salmonids. *Transactions of the American Fisheries Society* 129, 1360–1366. doi:10.1577/1548-8659(2000)129<1360
- Zeale, M. R. K., Bennitt, E., Newson, S. E., Packman, C., Browne, W. J., Harris, S., Jones, G., and Stone, E. (2016). Mitigating the impact of Bats in historic churches: The response of Natterer's Bats *Myotis nattereri* to artificial roosts and deterrence. *PLoS ONE* 11, 1–23. doi:10.1371/journal.pone.0146782
- Zeale, M. R. K., Stone, E. L., Zeale, E., Browne, W. J., Harris, S., and Jones, G. (2018). Experimentally manipulating light spectra reveals the importance of dark corridors for commuting bats. *Global Change Biology* 24, 5909–5918. doi:10.1111/gcb.14462
- Zhang, F. S., Wang, Y., Wu, K., Xu, W. Y., Wu, J., Liu, J. Y., Wang, X. Y., and Shuai, L. Y. (2020). Effects of artificial light at night on foraging behavior and vigilance in a nocturnal rodent. *Science of the Total Environment* 724, 114566. doi:10.1016/j.scitotenv.2020.138271
- Zhao, X., Zhang, M., Che, X., and Zou, F. (2020). Blue light attracts nocturnally migrating birds. *The Condor* 122, 1–12. doi:10.1093/condor/duaa002
- Ziegler, A. K., Watson, H., Hegemann, A., Meitern, R., Canoine, V., Nilsson, J. Å., and Isaksson, C. (2021). Exposure to artificial light at night alters innate immune response in wild great tit nestlings. *Journal of Experimental Biology* 224. doi:10.1242/jeb.239350

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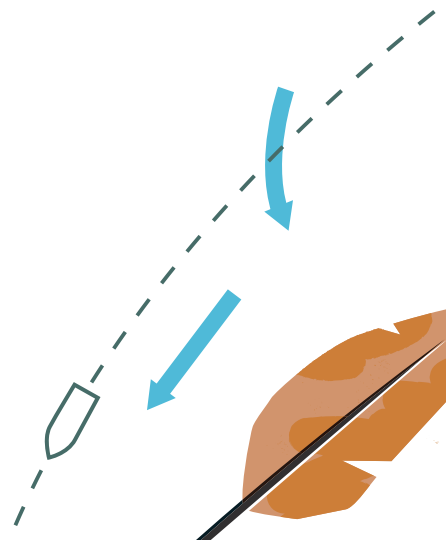
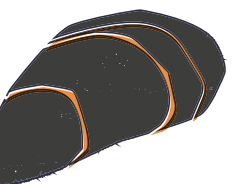
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