Attraction of nocturnally migrating birds to artificial light: The influence of colour, intensity and blinking mode under different cloud cover conditions

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ABSTRACT

A growing number of offshore wind farms have led to a tremendous increase in artificial lighting in the marine environment. This study disentangles the connection of light characteristics, which potentially influence the reaction of nocturnally migrating passerines to artificial illumination under different cloud cover conditions. In a spotlight experiment on a North Sea island, birds were exposed to combinations of light colour (red, yellow, green, blue, white), intensity (half, full) and blinking mode (intermittent, continuous) while measuring their number close to the light source with thermal imaging cameras.

We found that no light variant was constantly avoided by nocturnally migrating passerines crossing the sea. The number of birds did neither differ between observation periods with blinking light of different colours nor compared to darkness. While intensity did not influence the number attracted, birds were drawn more towards continuous than towards blinking illumination, when stars were not visible. Red continuous light was the only exception that did not differ from the blinking counterpart. Continuous green, blue and white light attracted significantly more birds than continuous red light in overcast situations.

Our results suggest that light sources offshore should be restricted to a minimum, but if lighting is needed, blinking light is to be preferred over continuous light, and if continuous light is required, red light should be applied.

1. Introduction

A considerable proportion of birds migrate at night and depending on topography part of such movements take place across marine areas. Over the last 150 years, it has been repeatedly reported that artificial sources of lights can attract birds crossing the sea at night as well as nocturnally foraging seabirds (Ballasus et al., 2009; Gauthreaux and Belser, 2006; Montevecchi, 2006; Ronconi et al., 2015). First observations of such attraction came from lighthouses, but also other sources of light such as ships, offshore platforms and various vertical constructions at land can have the same effect (Ballasus et al., 2009; Gauthreaux and Belser, 2006). Nocturnally migrating birds are attracted on a broad-scale to lit areas (McLaren et al., 2018). Most observations of attraction on land coincided with the finding of casualties, i.e. birds which collided with the lights or other parts of the vertical structures (Kerlinger et al., 2010; Longcore et al., 2013). Additionally, passerines flying over sea might deplete energy reserves when circling around lit structures (Jones, 1980). Systematic investigation of the literature revealed that

often specific weather conditions (e.g. heavy clouds, fog, drizzle) are responsible for concentrations around artificial lights (Ballasus et al., 2009; Ronconi et al., 2015). Birds use the stars for orientation during migration (Able and Able, 1996; Wiltschko and Wiltschko, 2003, 2009). Therefore, overcast may impair the orientation of nocturnal migrants (Bolshakov et al., 2013; Zhao et al., 2014) and thus influence the attraction to light. Despite many anecdotal evidence of bird attraction to light, a systematic long-term study investigating the effect of different light characteristics in combination with environmental factors potentially influencing behaviour of migrating birds is missing so far.

Forced by climate change, the late 20th century saw a rapid increase of renewable energy generation, and in the early 21st century more and more wind farms were planned and constructed at sea. Offshore wind farms (OWF) are illuminated at night for safety reasons regarding maritime traffic and aviation. Given the large amount of sea area covered (approx. 1900 km^2 in the northern half of Europe (between Ireland and Finland) by October 2017; http://www.4coffshore.com/), wind farming has caused a tremendous and continuing increase of artificial

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light in the marine environment. This adds to the existing lighting of numerous oil and gas platforms. Measuring the actual rate of collisions at offshore wind turbines is almost impossible (Desholm et al., 2006). However, as concentrations of migrating birds have been detected around OWFs at night with various methods (Hill et al., 2014), it became clear that measures to avoid fatalities will be desirable and the way of illuminating wind turbines at sea came into the discussion.

Visual perception of the environment differs between birds and humans (Martin, 2011). The birds' eye typically contains one rod and four different cone visual pigments, extending the visual spectrum into the UV range. Additional pigmented oil droplets enhance the ability for colour discrimination (Hart, 2001). Thus birds are able to distinguish between light colours and might react differently to them. Birds use several mechanisms and cues for long distance navigation and the exact involvement is still unclear (Mouritsen, 2018), but it is likely that visual cues (stars, landmarks) play an important role in guiding birds during nocturnal migration (Martin, 1990). Nevertheless, Martin (1990) suspects that migrating birds do not gain more visual information during the night than humans.

This study aims to disentangle the complex connection of light characteristics, which potentially influence the reaction of nocturnally migrating birds to artificial light under different cloud cover conditions. It is the first systematic study able to differentiate effectively between the influence of colour, intensity and blinking mode of illumination on the attraction of birds to light (see Section 4. Discussion). We took a human perspective for our study, in other words we analysed the effect on birds of illumination designed for the human eye and thus differentiated the light characteristics by human perception. In an experiment more than 20 km off the mainland on a North Sea island, nocturnal migrants were exposed to different combinations of light colour, light intensity and blinking mode while measuring their number close to the light source with thermal imaging camera recordings. Current safety regulations forbid alteration of the illumination of vertical artificial structures and we thus concentrated on bird attraction to an experimental light setup rather than on bird fatalities. Focusing on passerines as the largely dominating group in our recordings, we first tested the overall attracting effect to artificial light for nocturnally migrating passerines under different overcast conditions. Further, we analysed whether certain combinations of light colour, intensity and blinking mode were particularly more or less attractive to these birds, when cloud cover was either dense or when stars were visible. In a last step, we aimed at disentangling the overall underlying effect of either light intensity, blinking mode or a certain light colour in overcast conditions. This study took a conservation angle and was conducted to gain insight into an optimal solution for the nocturnal illumination of OWFs with respect to minimize the number of bird attractions and consequently the collision risk.

2. Materials and methods

2.1. Study area

The experiment was conducted in autumn 2013 (30 September–28 October), spring 2014 (10 February–13 May) and autumn 2014 (27 September–3 December) near Hörnum in the south of the island Sylt, which is situated in the German Wadden Sea (54° 47′ N, 8° 17′ E; Appendix Fig. A1). The technical equipment was installed on top of a container in 100 m distance from the coastline, 15 m above sea level. No artificial light was present in close proximity to the study site. The distance between the study site and the village Hörnum was 2 km, the Hörnum lighthouse was 5 km away.

Assuming departures from the North Sea coast of Lower Saxony in spring and from Norway, Sweden or the Danish North Sea coast in autumn, respectively, migratory birds passing the study site have already flown at least several dozens of kilometers above sea and can be assumed to represent relevant flight altitudes and typical flight behaviour for sea crossings during migration.

2.2. Experimental setting

At the study site, two colour change spotlights (Futurelight OFL-72 K2 3W, LED technology) were installed less than 1 m apart (Appendix Fig. A2), heading to the sea in a vertical angle of 45° to west/southwest (spring) and north/northwest (autumn), respectively, i.e. against the expected main flight direction. The characteristics of the colours used are listed in Table A1 (in Appendix). Yellow was obtained by mixing green and red (R: 255, G: 070), while white resulted from the mixture of all RGB LEDs in equal proportions. All applied colours lie within the visible range of birds between 300 and 700 nm (Osorio and Vorobyev, 2008). Light intensity was adjusted for all colours in a way that a luxmeter (Testo 540, reference class 3, DIN 5032 part 7) in 1 m distance in front of both spotlights measured 6800 lx with full intensity and 3400 lx with half intensity. As the experiment was supposed to give significant results within short time, a light intensity higher than the one used at OWFs was chosen. However, in contrast to the spherical obstruction lighting of offshore wind turbines the used LED-spotlights had a directed opening angle of 50°. This narrow opening angle directing to the sea prevented attraction of non-migrating birds from the island. For the discussion of our results we recalculated the light intensities measured in lx into total irradiance in W/m^2 for each light colour, by taking into account the specifications of the used LEDs, the spectral-specific sensitivity of the lux-meter as well as the luminance efficiency of the different wavelengths. Subsequently the relative sensitivity of avian rods (Hart et al., 2000) was used to discuss the perception of this eye-independent measure of the brightness of the different colour and intensity combinations for birds.

Two thermal imaging cameras with different focal length (AXIS Q1922 E 10 mm und 35 mm, 30 FPS) were installed parallel to the spotlights in 2 m distance, directing 45° upward. This camera system allowed us to record flying birds independent of light, i.e. also during periods with spotlights switched off. The applied telephoto lens covered a larger recording distance than the wide angle lens.

Further, long-exposure images from a panoramic camera (MOBOTIX M24M-Sec-Hemispheric; objective: N11) with an angular field of 180° combined with information from a video camera (Arecont Vision AV3130) were used to determine whether stars were visible, as a proxy for cloud cover. In these long-exposure images even dimmer stars are visible in a bright surrounding. Background illumination by the moon might potentially influence the reaction of birds to artificial light, with the absence of the moon leading to stronger attraction (Bolshakov et al., 2013; Verheijen, 1980). Combining information on the moon phase with its presence on the sky and the coverage of the moon by clouds showed that, as expected by the dependence on the natural lunar cycle of the amount of time the moon is on the sky during a night, independent of the light variant the majority of our bird-positive images were recorded when the moon was absent, covered by clouds or had a very small disc (Appendix Fig. A12). Only 15% of the data came from minutes with visible moon not surrounding new moon. For simplicity, given the small variation in the percentage of bird positive images between light variants as well as darkness within the different moon categories (Appendix Fig. A12), we thus did not include the moon into our detailed analyses here. To control the function of the spotlights externally a light meter (Sky-Quality-Meter, SQM-LE) was used to record the actual light intensity.

Finally, bird calls were recorded throughout the experimental periods with a directional microphone (Sennheiser MKH 110), which was installed in a wind shield. Audio signals with a frequency above 1500 Hz were automatically stored on a computer and later identified by an experienced field ornithologist (Hill and Hüppop, 2008). These recordings were used to gain deeper insights into the species composition migrating at the study site and the behaviour of certain species.
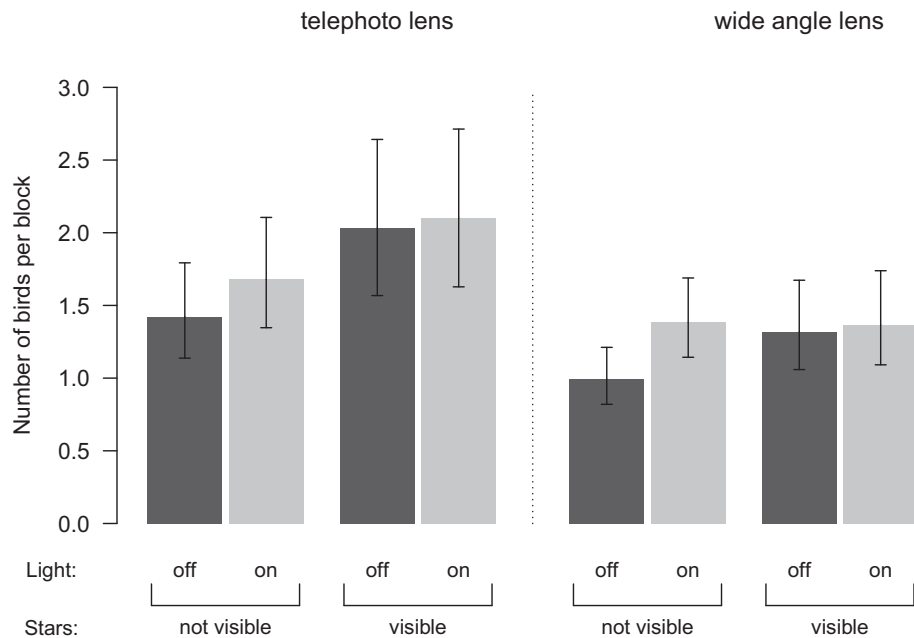
Fig. 1. Modelled number of birds per 15 min intervals for autumn 2014 (with 95% credible intervals) recorded with the two different thermal imaging camera lenses when spotlights were switched on or off under conditions where stars were either visible or not.

2.3. Experimental design

Since it was not possible to draw conclusions of the active light regime from any recording, bird or call numbers were logged by the analysts independently from any expectations. During the study periods, from the beginning of the evening to the end of morning nautical twilight (sun 12° below horizon) a total of 20 light variants (Appendix Fig. A3) were supplied at random for 15 min each. Successive light blocks were separated by a 15 min break of darkness. Each colour (blue, green, yellow, red, white) was emitted once with full (6800 lx) and half intensity (3400 lx), both as constant and blinking light (1 s on, 1 s off, i.e. 30 flashes per minute). In nights exceeding 10 h, the sequence of light variants was repeated until nautical twilight, whereas in nights shorter than 10 h (especially during spring migration) not all light variants could be applied in each night.

Video frames from the thermal imaging cameras were added up within each minute, thus supplying images of flight tracks (max. 60 images per hour). These images were divided into bird positive and bird negative ones. The analysis concentrates on nocturnal passerine migration of single individuals and thus bird positive images showing large birds or flocks were not included. Based on recorded bird calls passerines represent the majority of migrants at our study site (Appendix Table A5) and were the primary collision fatalities at an offshore research platform in the North Sea (Aumüller et al., 2011; Hüppop et al., 2016).

Information on cloud cover (stars visible or not) were added to the bird positive images or call positive minutes.

2.4. Statistical analysis

To analyse the number of birds recorded in the thermal imaging video frames or the number of audio files with bird calls we applied Generalized Linear Mixed Models (GLMM) with a Poisson error distribution and log-link function. The models were run in the statistic program R (R Development Core Team, 2014) with the function "glmer" from package "lme4" (Bates et al., 2014). Simulations to generate credible intervals for the model parameters were conducted with function "sim" from the package "arm" (Gelman and Su, 2014). Data from the two thermal imaging cameras (wide angle lens and telephoto lens) were analysed separately. The sound data of the three most common species in our data set were evaluated in different analyses.

The number of individually flying small birds was summed over each 15 min block of light or darkness, considering only blocks with images from at least 14 min. For the sound recordings the number of audio files with bird calls, as a proxy for the number of recorded birds, was also summed over each 15 min block. For both data types only combined 30 min light/darkness blocks with at least one recorded bird in one of the corresponding blocks were included in the analysis. Combined light/darkness blocks without birds were excluded, because these were most likely periods without migration at the study site.

Light on/off: Our first analysis compared blocks with activated light to blocks with light switched off in order to test the overall attracting effect of light compared to darkness on migrating passerines. This was the only approach also applied to the audio data, because of the smaller sample size compared to the visual data.

Light variants vs. off: To distinguish between light variants we used a second approach. Here we compared individual light variants and darkness. Each combination of intensity, blinking mode and colour was given a separate encoding. This resulted in 20 encodings for light (see Appendix Fig. A3) and another encoding for darkness. The 20 light encodings were compared to each other and to darkness. As each of the 20 light variants consisted of several light parameters, it is not possible to assign observed effects to intensity, blinking mode or colour of the light.

Light specification: In order to distinguish between the effects of intensity, blinking mode or light colour we conducted another analysis of blocks when light was switched on only, i.e. without comparison to darkness. Referring to the results from the previous modelling approaches (Figs. 1 and 2), the data set was limited to those blocks where stars were not visible.

Nocturnal migration intensity is highly variable between nights. Since several 15 min blocks were recorded in one night, the GLMMs included the migration night as a random effect to account for the fact, that data within one night are more similar than between nights. Since each 15 min light block was associated in the experiment to the following 15 min block of darkness, the combined 30 min block was treated as an additional random effect in the models where blocks of light and darkness were included.
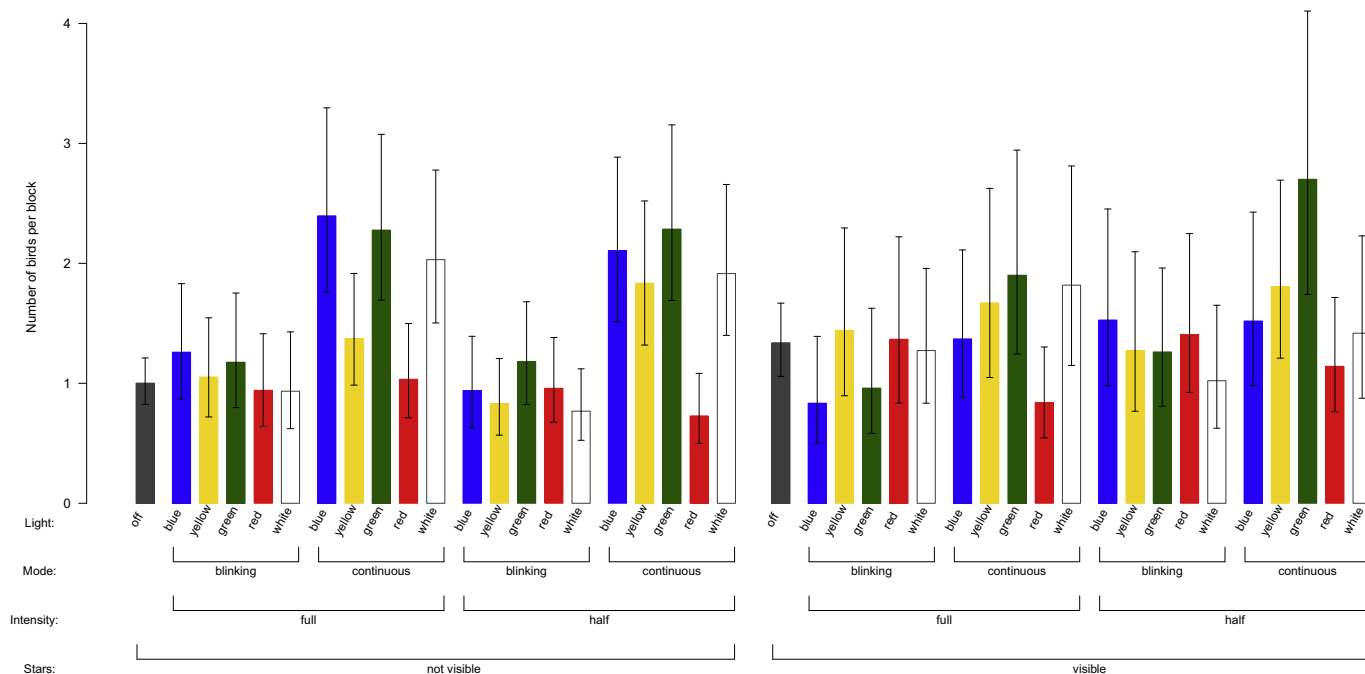
Fig. 2. Modelled number of birds per 15 min intervals for autumn 2014 (with 95% credible intervals) recorded with the thermal imaging camera with a wide angle lens for the different light variants and when spotlights were switched off under conditions where stars were either visible or not. (For a coloured variant of this figure, the reader is referred to the web version of this article.)

The light characteristic (i.e. light on/off or the 21 light encodings depending on the analysis) was included in the models as a categorical fixed effect. Other categorical fixed effects were migration period (autumn 2013, spring 2014, autumn 2014) and visibility of stars (stars visible or not visible). Due to the small number of audio recordings in spring 2014 this migration period was excluded from the analyses. For the visibility of stars we differentiated whether stars were predominantly seen in video images from minutes with recorded birds within a combined 30 min light/darkness block (i.e. was classified as visible stars). Further, we included the two-way-interaction of the light characteristic and the visibility of stars into the model. A stepwise backward elimination of terms in the models was applied, where the decision was based on a significance level of 0.05 in a likelihood-ratio-test.

The data were tested for overdispersion and if necessary supplemented by a random effect, which has as many factor levels as the number of observations. A difference of at least two in the Bayesian Information Criterion (BIC) was used as decision criterion when comparing the fully saturated model with and without the additional random effect.

As a measure of variability, 95% credible intervals for parameters were calculated based on simulated posterior distributions using posthoc MCMC (Markov Chain Monte Carlo) procedures with 2000 simulations. The result figures give 95% credible intervals of the predictions, which allow identifying the differences between individual combinations of treatment levels directly.

3. Results

3.1. Light on/off

For both thermal imaging cameras (sample sizes obtained from the three observation periods are given in Appendix Table A2), the model fitting the data best was the full model, including light (on/off), visibility of stars, and the two-way-interaction of light and stars as well as the migration period as fixed effects (Appendix Table A3). Both data sets showed overdispersion (BIC: wide angle lens - 12,054.82 (with observation level), 13,073.59 (without observation level); telephoto lens - 16,626.49 (with observation level), 17,134.34 (without observation level)), therefore an observation level random effect was included in the models.

The results for both cameras showed that the frequency of migrating passerines was higher in autumn than in spring. Given that the highest number of birds passed our study site (Appendix Table A2) in autumn 2014 and that the results for the three migration periods differ only in magnitude, our figures for all following results represent this migration period (Fig. 1) and the figures for the remaining periods are given in the Supplementary material (Appendix Figs. A4 and A5). When the spotlights were switched off, both cameras recorded more birds when stars were visible than under cloud cover conditions, which reflects the general migration pattern well. As expected, the telephoto lens recorded more birds per block than the wide angle lens (Fig. 1), which covers a comparatively smaller distance. The camera with the wide angle lens revealed that in overcast situations more birds per block were recorded when the spotlights were switched on compared to intervals of darkness (Fig. 1, Appendix Figs. A4 and A5). This difference did not occur when stars were visible. The results for the camera with the telephoto lens do not reflect the difference for lights on and off under conditions with cloud cover. The recorded distance seems larger than the range where birds are potentially affected by light. Therefore, we restricted the detailed analyses to the camera with the wide angle lens.

3.2. Light variants vs. off

When the different light variants were introduced into the analysis, the model fitting the data best for the thermal imaging camera with the wide angle lens was again the full model, including 20 individual light variants and darkness, visibility of stars, and the two-way interaction of light and stars as well as the migration period as fixed effects (Appendix Table A3). Due to overdispersion (BIC: 12,194.59 (with observation level), 12,837.65 (without observation level)) an observation level random effect was taken into account.

The analysis for the different light variants versus darkness confirms

the general results from the model considering only light on and off (Fig. 2, Appendix Figs. A6 and A7). When light is switched off, more birds per block were recorded when stars were visible compared to conditions when stars were not visible. While certain light variants differed from darkness in overcast blocks, this difference disappeared when stars were seen. The only exception is continuous green light of half intensity. When stars were not seen, green, blue and white light showed a higher number of birds per block when continuous light was applied compared to darkness, while this was not the case for red light. Under these overcast conditions, fewer birds per block were recorded in continuous red light (full and half intensity) than in blue, green and white light. Yellow light showed an incoherent pattern, with a lower bird frequency compared to green, blue and white light, when continuous light of full intensity was deployed, but not with half intensity. None of the blinking light variants differed from darkness, when stars were not seen in the recorded images.

3.3. Light specification

When restricting the data set for the wide angle camera to those images of minutes in which stars were not visible the model fitting the data best included blinking mode, light colour, and the two-way interaction of blinking mode and colour as well as the migration period as fixed effects (Appendix Table A4). Due to overdispersion (BIC: 4211.53 (with observation level), 5578.95 (without observation level)) an observation level random effect was again taken into account.

The analysis of the light specification supported the preceding results (Fig. 3, Appendix Figs. A8 and A9). Light intensity does not determine the number of birds attracted. For all light colours, except red, more birds per block were recorded when continuous light was applied compared to blinking light. The number of birds recorded did not differ between red continuous and blinking light, but red continuous light attracted significantly less birds than continuous light of any other colour. Under yellow continuous light fewer birds were recorded than under green and blue continuous light. When blinking light was applied the attracting effect did not differ significantly between light colours.

3.4. Flight call recordings

Many species utter flight calls during nocturnal migration (Farnsworth, 2005) and previous studies showed that the general night-to-night migration patterns of sound recordings correlate with radar data, thermal imaging and mist net trappings (Farnsworth et al., 2004; Horton et al., 2015; Sanders and Mennill, 2014). In our experiment, the majority of calls were from redwings *Turdus iliacus*, song thrushes *T. philomelos* and common blackbirds *T. merula*, showing that thrushes dominate the nocturnal migration at the study site (Appendix Table A5). For redwings and song thrushes nocturnal flight calls were generally more often recorded during periods of illumination than during darkness, although this effect was not significant in autumn 2013 for the redwing (Appendix Fig. A10). Common blackbirds showed an attraction to light only when stars were not visible.

All three models included an observation level random effect due to overdispersion (BIC: redwing - 1742.86 (with observation level), 1857.10 (without observation level); song thrush - 718.23 (with observation level), 733.68 (without observation level); common blackbird - 480.74 (with observation level), 504.76 (without observation level)). The model fitting the data best for the redwing included light on/off and the migration period as fixed effects, the best fitting model for the song thrush considered only light while the best fitting model for the common blackbird contained light, the visibility of stars and their interaction (Appendix Table A6).

4. Discussion

Following numerous observations of birds being attracted to artificial lights at night (Ballasus et al., 2009; Gauthreaux and Belser, 2006), this study is to our knowledge the first systematic evidence over several migration periods that even relatively weak sources of light compared to others in the distant surrounding (e.g. light house, road and village; see Section 2.1. Study area) attract nocturnal migrants flying over sea. This result refers to passerines, of which most were thrushes in our study. Although more birds migrate when visibility is high, the influence of illumination is stronger in overcast conditions. Compared to blocks of darkness, more individually migrating passerines were recorded in blocks of experimental illumination when stars were not visible. The sound recordings for the three most common species in our study prove that attraction of birds leads them close to the sources of light, since the microphones record only in close vicinity. As celestial cues play a role in the orientation of birds migrating at night (Able and Able, 1996; Wiltschko and Wiltschko, 2003, 2009), nocturnal attraction to light might be connected to the amount of available sources for orientation and therefore varies with respect to prevailing environmental condition (here: overcast). Stronger attraction to artificial light (measured by collision numbers) during nights with cloud cover compared to nights with clear skies was identified in earlier studies (Brewer and Ellis, 1958; Graber and Cochran, 1960). Additionally, it has been shown that magnetic compass orientation of at least some passerine species
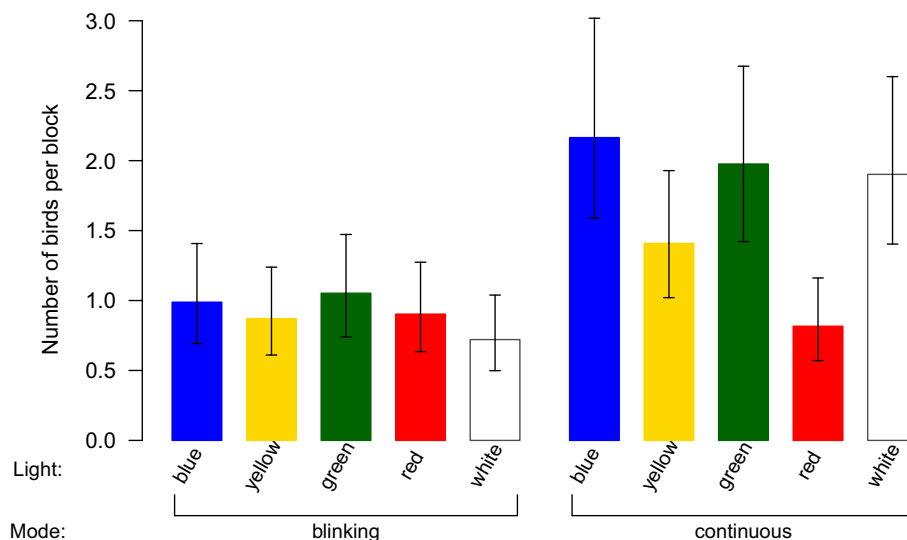

Fig. 3. Modelled number of birds per 15 min intervals for autumn 2014 (with 95% credible intervals) recorded with the thermal imaging camera with a wide angle lens for blinking and continuous light of different colour under conditions where stars were not visible. (For a coloured variant of this figure, the reader is referred to the web version of this article.)

under laboratory conditions requires light of specific wavelengths (Wiltschko et al., 1993).

Given the extent of established oil and gas installations offshore as well as the existing and planned OWF construction in northern Europe and thus the potential of nocturnally illuminated offshore wind turbines and other anthropogenic structures in the marine environment to attract numerous birds, our study demonstrates the importance of the characteristics of the illumination. Such an attraction is connected to the risk of collision at vertical structures, especially if considering unlit and rotating blades, and a risk of depletion of energy reserves when circling around a light source. Therefore, it is important to know which light variant causes least attraction. The recordings of nocturnal flight calls in this study have shown that birds approaching the experimental site include many thrushes. Regarding found casualties, these species were identified to be particularly at risk to collide with illuminated offshore structures (Aumüller et al., 2011; Hüppop et al., 2016).

Under the prevailing weather conditions during the experiment, no light variant was consistently avoided by birds. Nevertheless, some but not all light variants attracted more birds than darkness. While the two intensities of light emission did not influence the number of birds attracted, our study showed that birds are drawn more towards continuous light than towards blinking illumination, when stars were not visible. The change in intensity was comparably small, and a difference of a higher magnitude might have an effect as an alteration of a lighthouse lamp suggested previously (Jones and Francis, 2003). The number of birds recorded did not differ between blocks with blinking light of different colours as well as compared to blocks of darkness. This is the first systematic evidence showing that intermittent light is less disturbing than continuous light for birds migrating nocturnally over open sea.

Support for this result comes from a laboratory experiment with European robins *Erithacus rubecula,* which showed significantly less phototactic reaction on blinking and flashing yellow light compared to continuous yellow light (Hill, 2005). Our result also corresponds to previous studies with various limitations quantifying collisions of nocturnal migrants at communication towers and wind turbines, observing flight behaviour at radio towers or recording flight calls in an experimental setting. These indicated intermittent (i.e. flashing or blinking red or white) light being less attractive than continuous light (Gauthreaux and Belser, 2006; Gehring et al., 2009; Gehring, 2010) or did not reveal differences between intermittent light (red and white) and darkness (Evans et al., 2007; Gauthreaux and Belser, 2006; Kerlinger et al., 2010). However, the studies comparing blinking and continuous light failed to separate intensity and blinking mode. Continuous lights were installed in addition to blinking lights, resulting in a higher number of lights as well as a combined effect of blinking and continuous light. White and red lights were included into the studies without considering potential effects of the colour rather than blinking mode (Gauthreaux and Belser, 2006; Gehring et al., 2009; Gehring, 2010). Different locations of towers or to control sites and varying heights of the compared communication towers are further limitations of these studies. Topography might be the cause for different migration intensity and can influence the collision risk (Longcore et al., 2008). Although grouped in height classes, the towers still vary in height, which was shown to influence the number of bird fatalities (Longcore et al., 2012). Kerlinger et al. (2010) compared illuminated and unlit wind turbines within wind parks, but illuminated turbines are unlikely to be distributed at random. Most of the preceding studies are based on avian collision fatalities and do not account for imperfect as well as varying recovery probability with site in their analysis (Gehring et al., 2009; Gehring, 2010; Kerlinger et al., 2010). The results of the only experimental setup by Evans et al. (2007) are based on one migration night per sequence of light variants and are merely descriptive without statistical analysis.

In addition to their limitations the studies are not directly transferable, because they were all conducted in the United States with a very different species composition than in Europe. Further, our study is the first in a coastal context, which is needed to draw conclusions on bird behaviour over sea. Given that passerines cannot land on water, they might behave differently when flying over land compared to sea crossings.

Red continuous light was the only exception that did not differ from the blinking counterpart in our field experiment, whereas continuous green, blue and white light attracted significantly more birds than continuous red light in overcast situations. Only yellow light did not show a concise picture. Our results correspond to those of Evans et al. (2007), who recorded less nocturnal migrants in continuous red light compared to green, blue and white under the same weather conditions. Contradicting results were obtained by Poot et al. (2008), who identified green and blue as the least attractive light colours in a field experiment, also at the North Sea coast. Compared to our study, Poot et al. (2008) measured flight directions rather than bird numbers, failed to control for light intensity and weather influence in their analyses (Ballasus et al., 2009) and suffer from a low sample size (only 391 birds seen in 41 nights). As green continuous light proved to be among the most attractive light variants to birds under overcast conditions in our study, this light colour should be regarded as disadvantageous. Evans (2010) proposed that sensitivity to wavelengths in the green spectrum might result in an enhanced conspicuousness.

The light intensity of the different colours in our study was equal to the human eye, but total irradiance varied between colours (Appendix Table A1). It is unclear in which distance to the light source the birds flew and thus whether only rods or also cones are relevant for their vision. Spectral sensitivity of the visual pigments in the rods is similar across bird species with an absorption maximum around 500 nm (Hart, 2001). If we assume that only rods were active, we could transfer the results to perception by the avian eye (Appendix Fig. A11). In this case the different colours would only be conceived as varying brightness. Perception of the red light is low, which underlines our results physiologically. For the avian eye the blue light should appear brighter than the light of the other colours, even when comparing half intensity blue light to full intensity light of any other colour, because the blue light has a high irradiance and is well perceived. However, the enhanced brightness is not reflected in the number of birds attracted. Further, if we compare each colour separately, intensity perceived by the bird still doubles if we change from 3400 to 6800 lx, but again without an effect on the number of birds. These considerations still lead to the conclusion that in the range of intensities we studied here, the light intensity was irrelevant. It appears that red blinking light presently used as obstruction light in aviation does not attract more birds than blinking light of other colour. Our results give therefore no reason to change the existing illumination to a different colour.

In this study, we take a conservation angle and intend to obtain the bird friendliest human oriented illumination of artificial structures. We did not specify light intensity and spectral characteristics in terms of the avian eye. This equally relevant physiological approach would require a different experiment in order to gain fundamental insights into bird vision.

In terms of the height in which obstruction lights are mounted on offshore wind turbines, our results combined with the previous indications for non-attraction of intermittent light or a preference of blinking over continuous light, cover all relevant heights of vertical structures from the ground up to over 277 m (Evans et al., 2007; Gehring et al., 2009; Gehring, 2010; Kerlinger et al., 2010). Thus, there is no reason to assume that the results cannot be transferred to offshore wind turbines. As already described in the methods, we chose a study site where birds were assumed to have already flown at least several dozens of kilometers above sea before reaching the location in order to capture offshore migration behaviour as much as it was logistically possible. Nevertheless, it would be ideal to conduct an additional systematic light experiment at a remote offshore location to confirm our results. Although our study was specifically designed to gain

information on the behaviour of birds migrating over the sea, the implications might also be of importance for artificial structures on the mainland.

5. Conclusions

With respect to the current development of offshore wind farming we conclude that illuminated structures at sea generally attract nocturnally migrating birds under adverse weather conditions when orientation is potentially limited. Given the large number of offshore wind turbines as well as oil and gas installations operating in northern Europe and much more wind turbines being planned, minimizing attraction and thus the number of expected fatalities is highly advisable. The results from this study suggest that restricting the light sources offshore to a minimum is preferable. Illuminating the structures only when ships or aircrafts are approaching might be an option. In general, blinking light is to be preferred over continuous light, but if continuous light is needed, red light should be applied.

Conflict of interest

The authors have no competing interests to declare.

Data availability

All relevant data are available from the Mendeley data repository http://doi.org/10.17632/c4szbkbgyk.1.

Appendix A. Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.biocon.2019.02.029.

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