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Contents

1 Introduction

1. The following papers have been provided at the request of the Examining Authority in their first written questions (PD-011; Reference 1BEM50):

- **Factors influencing Manx Shearwater grounding on the west coast of Scotland (Syposz *et al*., 2018)**
- **The effect of light pollution on orientation in Manx shearwaters (Puffinus puffinus) (Syposz, 2020**)

2 Factors influencing Manx Shearwater grounding on the west coast of Scotland (Syposz *et al*., 2018)

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Factors influencing Manx Shearwater grounding on the west coast of Scotland

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Grounding of thousands of newly fledged petrels and shearwaters (family Procellariidae) in built-up areas due to artificial light is a global problem. Due to their anatomy these grounded birds find it difficult to take off from built-up areas and many fall victim to predation, cars, dehydration or starvation. This research investigated a combination of several factors that may influence the number of Manx Shearwater *Puffinus puffinus* groundings in a coastal village of Scotland located close to a nesting site for this species. A model was developed that used meteorological variables and moon cycle to predict the daily quantity of birds that were recovered on the ground. The model, explaining 46.32% of the variance of the data, revealed how new moon and strong onshore winds influence grounding. To a lesser extent, visibility conditions can also have an effect on grounding probabilities. The analysis presented in this study can improve rescue campaigns of not only Manx Shearwaters but also other species attracted to the light pollution by predicting conditions leading to an increase in the number of groundings. It could also inform local authorities when artificial light intensity needs to be reduced.

Keywords: light pollution, moon, probability model, *Puffinus puffinus*, random forest classification, Scotland, seabirds, weather condition.

Worldwide, many different species of animals are disturbed by artificial light pollution (Gaston *et al.* 2013). It can increase activity during the night (Dominoni *et al.* 2014), restrict or change patterns of movement of light-avoiding species (Frank 1988, Kuijper *et al.* 2008), influence reproductive phenology (Dominoni *et al.* 2014), disturb circadian patterns (Reiter *et al.* 2009) and cause fatal disorientation or attraction to the source of light (Verheijen 1960, Le Corre *et al.* 2002). One major group influenced by artificial light pollution comprises birds that show nocturnal activity, such as petrels and shearwaters (family Procellariidae; Rodríguez *et al.* 2017). Recent studies have found that seabirds are more likely to be encountered in locations with high light intensity (Le Corre *et al.* 2002, Rodríguez & Rodríguez 2009, Rodrigues *et al.* 2012, Troy *et al.* 2013, Rodríguez *et al.* 2015). Fledglings on their first flight are often found to crash-land in the cities and towns near their nest-sites; this phenomenon can be termed 'grounding' (Le Corre *et al.* 2002, Rodríguez *et al.* 2014) or 'fallout' (Ainley *et al.* 2001, Troy *et al.* 2011). Seabirds that land on the ground are often unable to take off from these urban locations due to their specialized anatomy, exemplified by legs set far back on the body to facilitate diving. However, this 'forward heavy' anatomy requires a slope or a gust of wind to be able to take off. Thus, if a grounded bird is not helped, it may fall victim to predation, dehydration, starvation or being hit by a vehicle (Telfer *et al.* 1987).

Even though the biological bases causing seabirds to ground are not fully understood, several patterns have been described across the family Procellariidae. Adverse weather conditions and

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moonless nights were reported to increase seabird fallout (Phillips & Lee 1966, Imber 1975, Reed *et al.* 1985, Telfer *et al.* 1987, Le Corre *et al.* 2002, Rodríguez & Rodríguez 2009, Miles *et al.* 2010, Rodríguez *et al.* 2014). A study by Rodríguez *et al.* (2014) also showed that strong winds blowing in the direction of areas of light pollution caused more seabirds to ground.

Like other birds from the family Procellariidae, Manx Shearwaters *Puffinus puffinus* encounter problems with light pollution (Brooke 1990, Rodríguez *et al.* 2008, Rodríguez & Rodríguez 2009, Miles *et al.* 2010). Manx Shearwaters are listed as least concerned by IUCN with an estimated population of more than 1 million individuals, but the majority of birds breed only on three islands – Skomer, Skokholm and Rum (Brooke 1990). In the current study we report grounding data collected during 6 years and investigate what factors influenced the number of Manx Shearwater groundings in the Scottish coastal village of Mallaig located close to the second largest colony of Manx Shearwaters (the Isle of Rum). A random forest model was developed that used meteorological variables and moon cycle to predict the daily quantity of birds that were encountered on the ground. Young petrels and shearwaters are inexperienced in flying and may be blown in the direction of a source of light, e.g. a village (Rodríguez *et al.* 2014). Therefore, we predict that the wind direction coming from Rum (westerly), as well as strong winds, causes the highest fallout. Similar patterns may be found due to visibility conditions; we predict that higher visibility would result in higher fallout, as the village of Mallaig might be seen by Manx Shearwaters from further away, causing more birds to be attracted to the light pollution. We further predict that the full moon results in a small number of grounded birds, due to the fact that the greater ambient light from the moon may cause a diminution of attraction to the artificial light (Reed *et al.* 1985). The random forest model presented allows exploration of each environmental variable and answers which of these has the greatest influence on the number of grounded Manx Shearwaters.

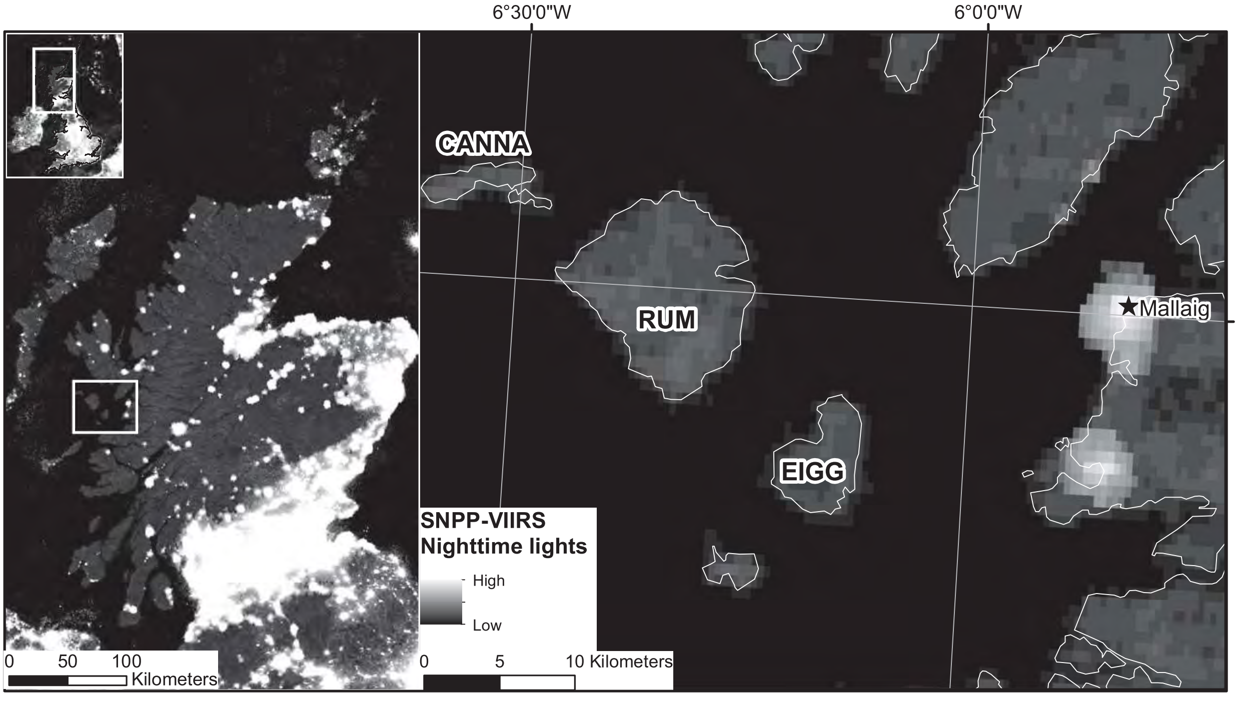

Figure 1. Artificial lights in the British Isles, the Isle of Rum and Mallaig. The left overview represents a night-time light map over the British Isles and Scotland in particular with the extent of the main map on the right (white box). The main map locates the village of Mallaig in relation to the Isle of Rum and how it accounts for a significant source of artificial light for the region. The night light is based on the Visible Infrared Imaging Radiometer Suite (Earth Observatory, 2012, Elvidge *et al.* 2013).

METHODS

Study site and Manx Shearwater grounding data collection

Mallaig (57°0′14.57″N, 5°49′52.36″W) is located on the west coast of the Scottish Highlands, 27 km east of the Isle of Rum (Fig. 1). The Isle of Rum harbours the second largest nesting site of Manx Shearwaters in the world with an estimated 76 000 pairs (Murray *et al.* 2003). Small numbers are reported to breed on the nearby island of Canna, in the region of 12–15 pairs (B. Swann, unpubl. data), and Eigg, with an estimated population of 50–150 breeding pairs (J. Chester, pers. comm.).

Manx Shearwaters from Rum leave the colony in late August and September (Brooke 1990). A volunteer-based project in Mallaig collected data between 2009 and 2014. Every day in September, at 22:00 h, at least one volunteer systematically checked Mallaig's harbour, going from Moorings Guest House to the outer harbour and back by foot (*c.* 2 km, Fig. 2) mainly in the harbour area (indicated by the black line). Additionally, the local community as well as other volunteers were involved in searches in other parts of the village. The local community is informed and reminded every year by posters and advertisements in the local paper about the possibility of grounded Manx Shearwaters.

When a bird was found, it was placed in a bird bag, then transferred to a suitable box and stored safely until the morning. The following day at 10:00 h, rescued birds were ringed and weighed. Manx Shearwaters were then taken on a ferry and released halfway between Mallaig and the Isle of Skye. The birds were released far from land, to avoid predation from Great Black-backed Gulls *Larus marinus* and European Herring Gulls *Larus argentatus*.

Predicting the number of grounded birds per day

To evaluate the influence of different environmental conditions on the number of birds grounded each night, a predictive model was developed using moon illumination, wind conditions and visibility. The total number of grounded birds reported across all of the surveyed area in Mallaig for a specific night was used in this analysis.

The wind, cloud cover and visibility variables for the period in which the birds are susceptible to grounding (month of September) were gathered for the years 2009–14 from the Met Office weather station located in Skye/Lusa (57°15′25.2″N, 5°48′32.4″W, 27.4 km north of Mallaig; Met Office 2006). The hourly data between 22:00 and 01:00 h BST was downloaded, as most of the rescue effort was during those hours. The wind direction was categorized based on the 16 compass directions. For each night, the weather was aggregated to calculate the average wind speed and visibility; for the wind direction, the mode for each night was extracted. In addition to the weather data from the Met Office, we also calculated the hourly moon illumination from the moon percentage derived from the oce R package (Analysis of Oceanographic Data, Kelley & Richards 2016). The value when the moon was below the horizon for the given time period was then set to 0, and when above the horizon, weighted by the cloud cover by multiplying the percentage of visible moon with factor proportional to the cloud coverage (in oktas between 1 for clear sky with no cloud cover and 0.5 for full cloud cover). This hourly weighted moon illumination variable was averaged for the time period and added to the weather data.

To predict the number of grounded birds during the month of September 2009 to 2014, a random forest algorithm was developed as a regression model, using the randomForest package in R (4800 trees; Liaw & Wiener 2002). The number of grounded birds for each night was predicted based on the aggregated weather data, the moon phase and the year. A random variable was also added as a 'noise' term representing the effects of influences not included in the model. By comparing the relative importance of the other variables in the model with this predictor, we could assess how they 'performed' in contrast to the 'noise' term. The accuracy of the model was estimated through a correlation between the observed and the predicted number of grounded birds. The latter was estimated from a random subset of the data that was excluded during the tree building iteration of the random forest ('out of the bag' prediction, Breiman 2001). This process, embedded in the algorithm, allowed us to discard the selection of training and test sets.

RESULTS

The number of grounded Manx Shearwaters varied from year to year and fluctuated within the month

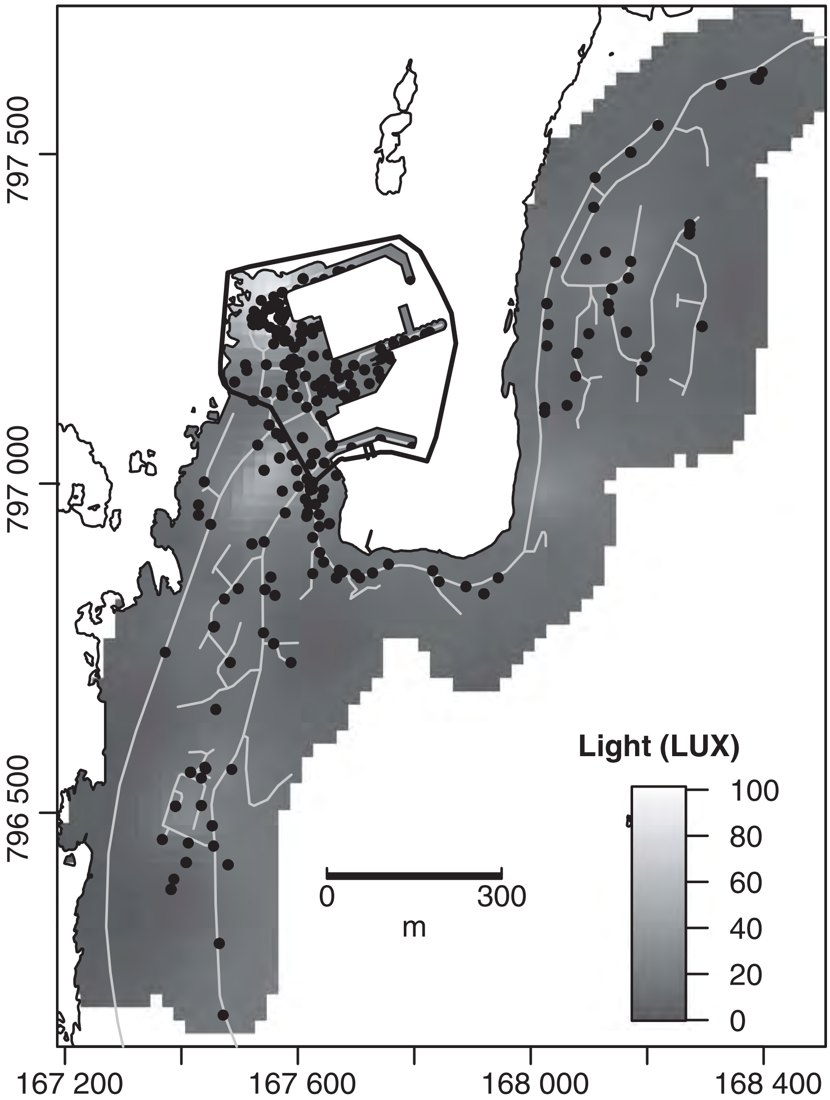

Figure 2. Spatial distribution of the grounded birds in relation to measured and estimated light intensities. The harbour area (delimited by a black line) contained most of the recovered birds. The road network is represented in light grey. The coordinates are in British National Grid panel easting and northing (metres).

(Table 1, Fig. 3a). Of the 1646 birds recorded between 2009 and 2014 included in the model, 45.0% were grounded during September 2012. The lowest fallout happened in 2011 with 4.6% of the total number of observed birds. The other years contained between 11.0% (2014) and 17.4% (2009) of the records. Most of the birds were found alive (92.2%) and were released successfully. Of the 1127 birds with known locations, 69.2% were found in the harbour area (Fig. 2, area indicated by black line), indicating a strong aggregation in that zone.

Predicting the number of grounded birds per day

When predicting the number of grounded birds in relation to the weather and moon cycle, the random forest algorithm explained 46.32% of the variance (with a mean squared residual = 197.71). Figure 4a represents the contribution of the different variables to the model; the year, the weighted moon percentage, the wind direction and the visibility all contributed more to the model compared

Table 1. Summary of numbers of grounded Manx Shearwaters each year between 2009 and 2014, showing the total number of birds ('Total') and birds that were found dead or that died before release due to an injury ('Dead'). 'Retraps' indicate the number of birds that were attracted to the light twice – they were ringed in Mallaig and came back after release.

Year	Total	Dead	Retraps
2009	287	29	0
2010	173	21	0
2011	75	9	0
2012	741	37	3
2013	189	20	0
2014	181	12	2
All years	1646	128	5

with the random noise variable. Other climatic variables were tested (temperature, rainfall, atmospheric pressure) but they did not lead to an increase in model performance or made lower contributions compared with the random variable. Figure 4b represents the significant relation between the observed and the predicted number of groundings ($F_{1,178} = 192.1$, $P < 0.01$), although the model tended to underestimate the number of groundings. Figure 5 represents the partial dependence plots for the different variables. These plots confirmed the exceptional number of groundings for 2012 and how low moon illumination and strong westerly winds increased the probability of groundings. To a lesser extent, both low and high visibility conditions contributed to a higher probability of groundings.

DISCUSSION

Difference between years, caused by the exceptionally high number of groundings in 2012, was the most important correlate of the variation in number of Manx Shearwater groundings in Mallaig. We also showed that the new moon and strong onshore winds were associated with an increase in probability of groundings. To a lesser extent, visibility conditions were also related to grounding probabilities. Our model, however, predicted just under half of the variance (46.32%) in the data, which might be due to other factors influencing grounding probabilities that were considered in our model or, more likely, to the coarse time resolution of the data.

We found that the grounding probability of Manx Shearwaters in Mallaig is best explained by differences between years, with a higher number of groundings in 2012 than in other years. Unfortunately, the population of Manx Shearwater on Rum and other nearby islands lacks yearly data on demography. However, the average productivity from colonies in Rum did not show statistically significant variations between 1986 and 2015 (JNCC 2016). The colony of Manx Shearwaters on Rum is 27 km away from Mallaig, and light pollution does not affect a high proportion of fledglings (maximum 741 grounded fledglings out of up to 76 000 fledglings, Murray *et al.* 2003, Table 1). Therefore, small variations in the number of fledged Manx Shearwaters on Rum are unlikely to have a strong influence on the numbers of grounded birds in Mallaig. Although during the fallout in 2012, moon phase and weather conditions tended to increase groundings (see below), the exceptionally high number of groundings that year is not completely explained by these environmental variables alone, as demonstrated by the high contribution of year in the model. This indicates that in addition to possible effects from population fluctuations, there may be other factors that were not included in the study, such as the concentration of food in the waters around Mallaig or attraction by sound (as suggested in Miles *et al.* 2010), or other factors not measured.

This study also found that variation in the number of grounded fledglings in Mallaig was related to the moon phase; in moonlit nights the number of grounded birds decreased. The same pattern has been observed by several other studies focusing on shearwaters and petrels (Imber 1975, Reed *et al.* 1985, Telfer *et al.* 1987, Le Corre *et al.* 2002, Rodríguez & Rodríguez 2009, Miles *et al.* 2010, Rodríguez *et al.* 2014). The reason for the moon influence was explained by the fact that a greater ambient light from the moon may cause a diminution of attraction to artificial light (Reed *et al.* 1985). Nevertheless, Le Corre *et al.* (2002) observed that grounded seabirds had longer wingspans and were lighter when the fledging period coincided with the full moon. This suggested the young seabirds stayed longer in their burrows because the full moon inhibits them from fledging. It is possible that both factors, the decreased activity of fledging, as well as the reduced attraction to the light, causes fewer groundings during the full moon. Further studies are needed to quantify the influence of each of these factors.

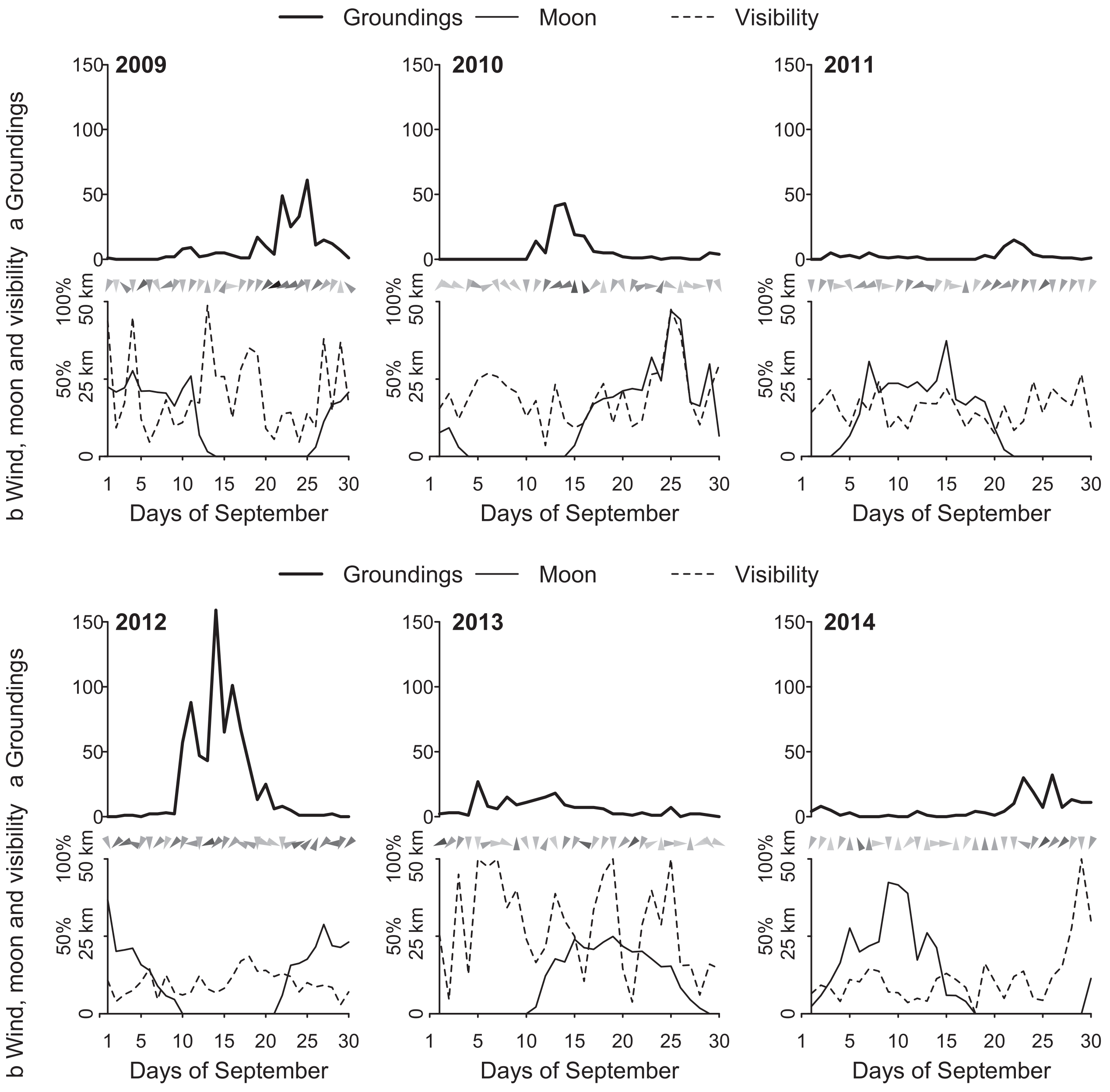

Figure 3. Daily distribution of the number of grounded birds (a, thick black line), wind (arrows), weighted moon illumination (b, thin black line) and visibility conditions (b, dotted line) between 2009 and 2014. The arrows represent the direction of the wind and darker arrows indicate stronger winds.

In addition to the influence of the moon and an important year effect, other climatic variables showed a strong effect when predicting the number of groundings. Onshore winds and strong winds contributed to higher probabilities of bird grounding. Extremes in visibility (high and low) also moderately increased the risk of grounding. Weather conditions can change very quickly during the 4-h window considered in this study. Aggregating the weather variables over the night means that some of the fine temporal scale changes were lost. In addition, it is difficult to match some short-term weather patterns with a specific bird grounding, as there may be a delay of several hours to even a few days between the moment when a bird was grounded and when it

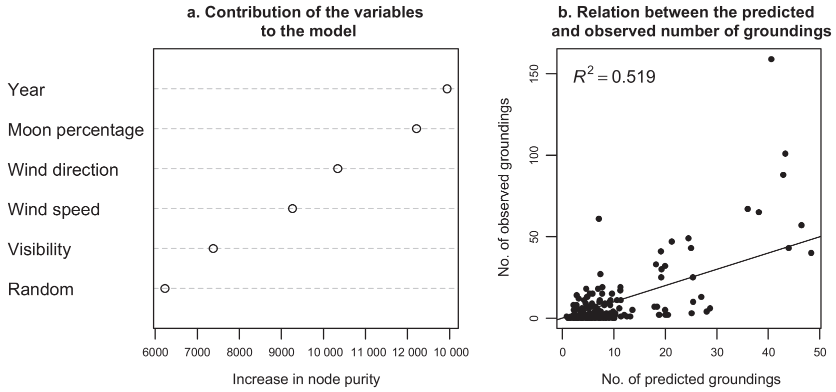

Figure 4. (a) Ranked importance of the different variables in the contribution of the prediction model for the number of bird groundings. (b) Correlation between the observed and predicted number of groundings.

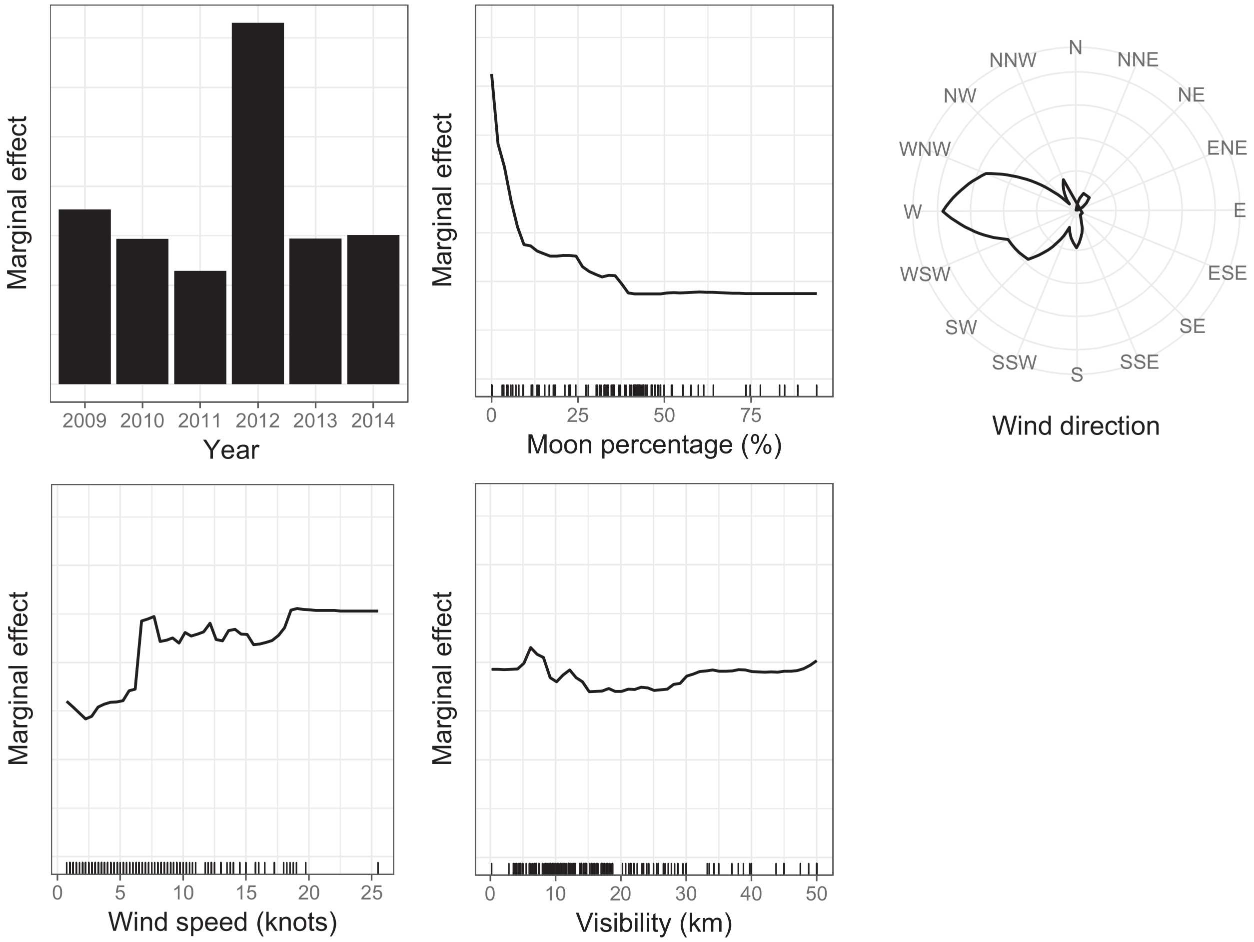

Figure 5. Partial dependence plots for the main variables contributing to the model illustrating the effect of the predictor variables on the fluctuations of the probability of bird grounding. On the polar plot for the wind direction (top right), the delimited area indicates the contribution of each wind direction to grounding probability.

was spotted and recovered (Rodríguez *et al.* 2012b, 2015). Similarly, there may be some delays between a change in weather pattern and a peak in groundings; these delayed effects are difficult to include in the model. The quantity of grounded birds is also influenced by the number of fledging birds and therefore more favourable weather conditions for fledging can cause higher numbers of groundings. The other main limitation of the model is related to multicollinearity, where some weather variables might be correlated, causing us to underestimate their individual effects.

The current study found a similar association between wind direction and grounding as the study of Rodríguez *et al.* (2014); the number of grounded Short-tailed Shearwaters *Ardenna tenuirostris* in that study was higher, with winds blowing from the colony to the artificial light pollution. It was suggested that birds might be blown away from the colony onto the roads. In other studies the breeding colonies were situated all around the coast or inland (Le Corre *et al.* 2002, Troy *et al.* 2011, Rodríguez *et al.* 2012a) and in these conditions it would be hard to test the effect that the wind direction has on groundings. The location of the Manx Shearwaters colony in Rum is to the west of Mallaig and the current finding confirms that strong winds blowing towards the source of light pollution causes the largest number of groundings. Rodríguez *et al.* (2014) found that the wind speed also had a positive influence on the risk of grounding, possibly because Short-tailed Shearwaters on flat Phillip Island, southern Australia, needed a gust of wind to facilitate their first flight. In our study area, westerly winds tended to be stronger than winds from other directions (average of 9.2 vs. 4.6 knots), indicating that low pressure weather systems might combine wind speed and direction effects leading to a higher risk of grounding. The burrows of Manx Shearwaters are situated on steep mountains (Mitchell *et al.* 2004) that allow birds an easier take-off. Thus, it is likely that the higher number of grounded birds during a strong westerly wind can be explained by inexperienced fledglings being blown in the direction of the light pollution in Mallaig.

An increase in the number of groundings can be expected when there are adverse weather conditions and cloudy, rainy nights (Phillips & Lee 1966, Telfer *et al.* 1987). This is possibly caused by increased light pollution due to rain, mist and clouds (Day *et al.* 2003). Nevertheless, a recent study by Wilhelm *et al.* (2013) did not detect any evidence for visibility influencing the fallout of Atlantic Puffin *Fratercula arctica*. This can be explained by the fact that more birds start their migration with clear sky conditions (Hüppop & Hilgerloh 2012). Our study confirmed both these trends presented in research by Phillips and Lee (1966) and Hüppop and Hilgerloh (2012), with slight increases in predicted grounding when the visibility was either low or high. Poor visibility was associated with strong westerly winds that were likely to disorientate and push the birds toward Mallaig. This is consistent with data obtained in this research, as it was found that visibility did not strongly contribute to the predictive model of the Manx Shearwater groundings.

Our study confirmed that more birds were grounded in nights with less moonlight (Reed *et al.* 1985, Telfer *et al.* 1987, Le Corre *et al.* 2002, Rodríguez & Rodríguez 2009, Miles *et al.* 2010, Rodríguez *et al.* 2014) and in nights with strong westerly winds (Rodríguez *et al.* 2014), showing that birds may be blown from their colony in the direction of the light pollution. Low and high visibility conditions also contributed to higher grounding probabilities. Thanks to these findings, rescue campaigns could focus their efforts on nights when the risk of groundings is highest or could inform local authorities under which conditions light intensity needs to be reduced.

We are deeply thankful to the communities of Mallaig, Morar and Arisaig, who kindly helped rescue Manx Shearwaters, and especially Victor Cruden, Sandy Maclaren, the local police and Steve MacDonald and family. We would also like to acknowledge Marine Harvest for their support, and the ferry company, Caladonian MacBrayne, who allowed us to release Manx Shearwaters from their ferry. We thank N. Harrison, P. Brown and S. Mowles for constructive comments on the manuscript and Anglia Ruskin University for its support.

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3 The effect of light pollution on orientation in Manx shearwaters (*Puffinus puffinus*) (Syposz, 2020)

The effect of light pollution on orientation in Manx shearwaters (*Puffinus puffinus*)

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ABSTRACT

Humans introduce artificial light at night (ALAN) to the landscape for many reasons - to facilitate commuting to work, to improve their safety and to enhance the nocturnal aesthetics of places. The resulting change in light levels distorts a cue which living organisms use. A cue which, otherwise, has been predictable for billions of years. While some animals adjust to or even take advantage of ALAN, other species respond negatively, with populations suffering due to the presence of artificial light. In particular, burrow-nesting seabirds struggle with light pollution located near to their colony, with thousands of juvenile birds landing in lit-up areas during fledging season – termed 'grounding'. The aim of this thesis is to investigate the behaviour of seabirds towards light pollution and, ultimately, to understand mechanistically the processes involved in grounding of seabirds. I explore, through observation and experimentation, the behavioural responses of an ALAN-susceptible seabird, the Manx shearwater (Puffinus puffinus) to artificial light. These experiments span the life-history stages of the Manx shearwater, from the orientation of juvenile shearwaters, before and during fledging, to the responses of breeding adults at the colony. I discover that the magnitude, but not direction, of behavioural reactions to artificial light is consistent across these life stages. At each life stage, reactions to ALAN appear to be related to the intensity and wavelength of light, the latter of which implies disruption of the visual system as a root cause of seabird grounding. Finally, in an applied study, I explore the effectiveness that updating old sodium pressure lamps with LEDs has had on shearwater grounding in a coastal town. Overall this thesis highlights the importance of understating the animals' behaviour towards light pollution at different life stages and locations, contributing to the evidence base for mitigation measures that might be implemented in future.

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For my family, whom I can always rely on.

I didn't fail 1000 times. The light bulb was an invention with 1000 steps.

Thomas A. Edison

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Chapter 1

General introduction

Introduction

For most of history, nights—especially moonless nights—were dark. However in the last 150 years human urbanisation has transformed our nocturnal landscape by changing natural light levels with illumination coming from streetlights, advertisement boards and other lighting installations (Falchi *et al.*, 2016). Artificial Light At Night (ALAN) has changed the night sky globally, and two thirds of Key Biodiversity Areas are affected by it (Garrett, Donald and Gaston, 2019). In areas polluted by light, it is estimated that more than 60% of nocturnal invertebrates species and around 30% of nocturnal vertebrates species could potentially be impacted (Hölker *et al.*, 2010). An extraordinary array of physiological and behavioural changes due to light pollution has now been documented on a variety of organisms (for general reviews of the impacts of ALAN on animals, see Longcore and Rich, 2004; Gaston *et al.*, 2013; Gaston and Holt, 2018; Owens and Lewis, 2018). Light pollution can affect the reproduction (Fobert, Da Silva and Swearer, 2019), communication (Owens, Meyer-Rochow and Yang, 2018), community structure (J. F. Wilson *et al.*, 2018), movement (Jung and Kalko, 2010) and behaviour (Yassumoto *et al.*, 2019) of many species and its effects are not limited to animals, with plants, fungi and bacteria also thought to be impacted (Dufresne, 1987; Yang *et al.*, 2019; Zhang *et al.*, 2020).

Among the numerous documented effects of light pollution on animals, its impact on movement can result in especially profound consequences manifesting in changes in the distribution of populations and ultimately drive species' decline (Rodríguez *et al.*, 2017; Owens *et al.*, 2020). On an individual level, ALAN can either cause positive phototaxis (attraction/misorientation towards lights) or negative phototaxis (determent/repulsion from lights). Mountain lions, spiders, bats, migratory birds and many species of insect are among those species where individuals have been found to avoid light pollution (Beier, 1995; Nakamura and Yamashita, 1997; Summers, 1997; Kuijper *et al.*, 2008; Cabrera-Cruz *et al.*, 2020). The converse phenomenon, positive phototaxis, can cause fatal collisions or entrapment of animals in a halo of light. Many species of nocturnal insects (review: Owens and Lewis, 2018), birds (Allen, 1880; Rodríguez *et al.*, 2017), frogs (Perry, Buchanan and Fisher, 2008), and turtles (Wilson *et al.*, 2018) exhibit profound attraction towards artificial light. The resulting restrictions and changes to animal movement caused by ALAN are of conservation concern since they might limit dispersal, decrease habitat connectivity and entrap animals in dangerous areas. It has therefore become essential to understand how light pollution impacts animals' behaviour so that we can effectively avoid or mitigate the negative impacts of light pollution on natural systems. With novel effects of light pollution on animals added to literature scope every year (Berge *et al.*, 2020; Cabrera-Cruz *et al.*, 2020; Shier, Bird and Wang, 2020), it is clear that a lot remains to be learnt.

How can movement be disturbed by ALAN in animals?

One way light pollution might affect the movement of animals is by disrupting their orientation abilities (Tuxbury and Salmon, 2005; Owens and Lewis, 2018). Nocturnally active animals are known to be able to orient using olfaction, visual landmarks, echolocation, earth's magnetic field or stellar objects such as stars, the moon and the Milky Way (Emlen, 1975; Papi, 1990; Wiltschko and Wiltschko, 2005; Lohmann, Lohmann and Endres, 2008; Warrant and Dacke, 2011; Dacke *et al.*, 2013). Reliance on objects emitting or reflecting light from the sky raises concern that in places where natural light levels at nights have been disturbed by human-made light sources, these orientation mechanisms could be impacted (Witherington and Martin, 2000; Rodríguez *et al.*, 2017; Van Doren *et al.*, 2017). Thus, providing a potential mechanism of interference whereby light pollution might impact individuals' fitness and/or population declines. While an extensive literature has focused on documenting detrimental outcomes of light pollution on many species (reviews: Longcore and Rich, 2004; Gaston and Holt, 2018), the efforts to explain the mechanistic basis of the phenomenon are rather limited and poorly tested and thus our ability to implement evidence-based mitigation is limited. Understanding more precisely how ALAN affects orientation in animals is therefore crucial.

To begin to understand the mechanistic impact of ALAN on animal movement, I propose here a simple framework in which we classify animal phototaxis into 'primary' responses to artificial light and 'secondary' responses to artificial light.

Secondary responses to light occur when animals use light as a cue for some other piece of previously learnt information. For example, animals may be attracted to light because they have learnt to associate it with prey availability (positive phototaxis), or conversely may be repulsed by it because it is associated with predation risk (negative phototaxis). Some species of bats (e.g. Jung and Kalko, 2010), birds (e.g. Robertson et al., 2010), and cane toads (e.g. González-Bernal et al., 2016) facilitate their hunting by congregating in places lit up by ALAN, leading to attraction-like behaviour. Following this attraction, animals may exhibit further behavioural changes. For example, cane toads (*Rhinella marina*) are observed to be more sedentary in lit-up areas, as the congregations of insects associated with increased light reduce the effort required by individuals to find food (González-Bernal et al., 2016). On the other hand, slow flying bats, like *Rhinolophus hipposideros*, and flightless nocturnal invertebrates called weta, have been found to avoid light (Stone et al. 2009; Farnworth et al. 2018). It has been suggested that these species are vulnerable to predation from animals that see better in light and thus avoid lit-up areas, including ALAN, to lower their risk of predation (Speakman 1991). Where artificial light intersects their normal foraging grounds, this avoidance behaviour could ultimately result in light-mediated fragmentation of their habitat, which has been linked to subsequent declines in population size (Owens et al. 2020).

Primary responses to artificial light involve an animal's orientation mechanism mistakenly taking the artificial light as a directional cue. Primary responses are known in at least two groups of animals, sea turtles and insects. Enthusiasts and researchers have long exploited the attraction of insects towards light through the use of light traps to collect specimens. The reaction towards light and its behavioural explanation depends on the species (Owens and Lewis, 2018). Some flying species approach the light directly, while others exhibit characteristic spiralling flight patterns. Some insects may sit under the light, looking stunned, while others try to stay in the vicinity of light, flying around it, frequently changing angular velocity and direction (Muirhead-Thompson, 2012). A possible explanation for why insects appear to orbit around lights was suggested in the form of the light compass theory (Baker and Sadovy, 1978; Sotthibandhu and Baker, 1979). If a flying insect maintains a constant angle towards the moon or stars, it could have an easy point of reference for maintaining a constant heading. Since ALAN has been introduced, lights are much closer than the celestial bodies, and if an insect maintains a constant angle towards a lamp, it will end up circling around it. Nocturnal bees and wasps provide examples for such behaviour. By adjusting their wings, they ensure that the top part of their visual field is brighter than the bottom one (Berry, Wcislo and Warrant, 2011). Conversely, those species that appear to be stunned under the light might be briefly or invariably deprived of sight. This could be explained by their visual system being highly sensitive towards light, causing saturation or structural degradation in their photoreceptors in particularly high light intensities (Meyer-Rochow, Kashiwagi and Eguchi, 2002; Honkanen *et al.*, 2017). Even if a dazzled insect escapes into darkness, it may be a long time before it is fully recovered (Bernhard and Ottoson, 1960).

The reasons for the attraction of marine turtles towards light have been also explored. In this group of animals, however, only hatchlings seem to be affected by light pollution (Salmon 2006). Young turtles hatch from a nest during the night and use brightness (Mrosovsky, 1967; Mrosovsky and Shettleworth, 1968; van Rhijn and van Gorkom, 1983; Tuxbury and Salmon, 2005) and elevation (Limpus, 1971; Salmon *et al.*, 1992) of the horizon as cues directing them to safety of the sea. In developed beaches, however, the brightness gradient is disturbed. Light pollution in coastal areas direct hatchling turtles away from the sea and towards dangers of towns and cities (McFarlane, 1963; Salmon, 2006; Bourgeois *et al.*, 2009). Turtles and insect are however not the only animals affected by light pollution. Birds are well-known to strongly react with positive phototaxis towards ALAN, but the mechanisms involved are not yet well understood. There are some emerging patterns, however, that might assist in revealing the answer.

Factors influencing the impact of ALAN on bird behaviour

Birds are mainly affected by ALAN during their migration, making them more susceptible to collisions with buildings (Loss, Will and Marra, 2015), predation (DeCandido and Allen, 2006) and changes to their stopover ecology (Lebbin *et al.*, 2007; Cabrera-Cruz *et al.*, 2020). Birds that spend energy to remain airborne around light might end up delayed for days on their migration route (Seewagen and Guglielmo, 2010) or die due to exhaustion (Ramirez *et al.*, 2015). Recent radar data have shown vast congregations of migrating birds around light polluted areas (Van Doren *et al.*, 2017; McLaren *et al.*, 2018; Horton *et al.*, 2019). The extent of the attraction has been found to be dependent on the duration, intensity and spectrum of the light.

There is no clear consensus on how the spectrum of light impacts birds' behaviour. Whereas Evans *et al.* (2007) and Zhao *et al.*, (2020) reported that red light caused less attraction in birds (mainly passerines) than blue and green light, Poot *et al.* (2008)(but see Evans (2010) for critisism of methodology) provided evidence that red light increased the chance of collision more than blue and green light. Many researchers have observed, however, a consistent pattern in birds' responses towards flashing light. Shorter light-on pulses seem to result in smaller numbers of affected birds, suggesting that a longer dark period allows birds to disperse away from the light polluted area (Tufts, 1928; Baldwin, 1965; Avery, Springer and Cassel, 1976; Wiese *et al.*, 2001; Evans *et al.*, 2007; Gehring, Kerlinger and Manville, 2009). Likewise, higher light intensity seems to result in increased bird congregation around lit-up areas (Verheijen, 1985; Jones and Francis, 2003).

Grounding in Procellariiformes: current knowledge.

Among birds, seabirds, especially species from the order Procellariiformes, seem to be particularly strongly affected by light pollution. Procellariiformes are pelagic seabirds with a range extending across all the world's oceans. They are mostly colonial, predominantly breeding on offshore or oceanic islands. Most members of the order have a 'forward heavy' anatomy that is adapted to life at sea but results in birds unable to walk well on the land. Their nests are generally located on cliffs or in burrows where a steep slope or a long runway allows them to take off again. Many species visit their nests during the night to avoid diurnal predators (Watanuki, 1986; Keitt, Tershy and Croll, 2004; Silva *et al.*, 2011).

Unlike passerines, seabirds cannot easily take off once they land in a light polluted area because of their anatomy. Buildings, cars and other structures form barriers from wind and a long runway necessary for take-off. If a seabird is left grounded on its own, it is vulnerable to predation by wild or domestic animals, as well as starvation, dehydration, or it can be hit by a car. Many rescue campaigns worldwide gather volunteers and communities to collect grounded birds. These campaigns not only release hundreds of seabirds back to the sea, but also collect valuable data on seabird groundings (review: Rodriguez *et al.*, 2017). The phenomenon of seabirds' congregations around light has a special term called "grounding" or "fallout" (Reed, Sincock and Hailman, 1985; Rodríguez *et al.*, 2017). 56 out of 113 burrow-nesting species of Procellariiform seabirds are reported to ground in light polluted areas near to their nesting site. Most of the grounded birds are fledglings; depending on species from 68% to 99% of grounded birds (Rodriguez *et al.*, 2017). Juvenile birds start their migration without adult conspecifics during the night. The light polluted area might be on the same island as the colony (e.g. Le Corre *et al.*, 2002) or kilometres away from it (e.g. Syposz *et al.*, 2018).

There is evidence that the severity of the grounding depends on several environmental factors. First, evidence suggests that moon phase influences the magnitude of seabird groundings. Several studies have found a strong correlation between the state of moon and the number of grounded birds (Imber, 1975; Reed, Sincock and Hailman, 1985; Telfer *et al.*, 1987; Le Corre *et al.*, 2002; Rodríguez and Rodríguez, 2009; Miles *et al.*, 2010; Rodríguez *et al.*, 2014; Syposz *et al.*, 2018), with fewer birds found during full moon and the highest number of grounded birds found during moonless nights. Second, some research revealed that weather conditions also play a role. Adverse weather conditions, i.e. cloudy and rainy nights, cause higher fallout (Telfer *et al.*, 1987), however this relationship has not been found in other studies (Syposz *et al.*, 2018). Rodríguez *et al.* (2014) and Syposz *et al.* (2018) also found that wind speed and direction have an influence on fallout, with stronger wind from the direction of a colony being associated with a greater number of birds grounding. This was explained by the fact that inexperienced fledglings can be blown in the direction of the light pollution. In studies where that relationship has not been found, the colony was located on the same island as the grounding events (Le Corre *et al.*, 2002; Troy, Holmes and Green, 2011; Rodríguez, Rodríguez and Lucas, 2012), presumably making it difficult to detect a similar effect.

Besides environmental conditions like weather and moonlight, the characteristics of the artificial light also affect the severity of seabird groundings. In particular, similar to collisions in other bird species, the intensity of light pollution can play an important role. Decreasing light pollution by reducing the spill of light or by simply turning lamps off results in a smaller fallout (Reed, Sincock and Hailman, 1985; Glass and Ryan, 2013; Rodríguez *et al.*, 2014), and therefore has been recommended as a mitigation measure against seabird grounding. However, one has to be cautions as the results might be species specific. Indeed, Miles et al. (2010) found that covering all the lights in a village decreased the number of grounded Leach's Storm- Petrels (*Hydrobates leucorhous*) but not of Manx shearwaters (*Puffinus puffinus*).

In addition to light intensity, the spectrum of light can influence the severity of the fallout. Red and yellow lights cause less grounding in Tropical Shearwaters (*Puffinus bailloni*) than green and blue lights (Salamolard *et al.*, 2001). Changing from white broadband to red and green lights reduced fallout of seabirds in Chile (reported in Rodriguez et al., 2017). Covering lamps with polarizing filters, however, did not seem to have any effect on Newell's Shearwaters (*Puffinus newelli,* Reed, 1987). Finally, a recent study by Rodríguez, Dann and Chiaradia (2017) investigated the effects of type of streetlights and found that metal halide, light emitting diode and high-pressure sodium lights resulted in different numbers of birds grounded. They concluded that high pressure sodium lamps are the best to use near to nests of short-tailed shearwaters (*Puffinus tenuirostris*). Completely changing the colour of artificial lights might not be the most practical way to address the light pollution problem in cities and towns. Thus, guidelines regarding new lights should consider practicality of their use for humans. Changing lights might be demanding and costly, therefore strong evidence should inform such conservation mitigation measures.

The mechanisms of seabird grounding

Despite many reports on the patterns of grounding in Procellariiform seabirds, the sensory mechanisms affected by light pollution are poorly understood. Understanding these mechanisms is however essential to produce robust, effective and evidence-based recommendations for conservation. The existing literature suggests two possible senses that can be disturbed by artificial light pollution resulting in grounding in Procellariiformes: light-dependent magnetoreception (proposed generally for birds: Evans *et al.*, 2007) and vision (Imber, 1975; Telfer *et al.*, 1987; Rodríguez *et al.*, 2017)**.**

Magnetically mediated light pollution effects

Magnetoreception, the detection of the magnetic field of the earth by animals, is known to be used by some bird species as a compass sense (Wiltschko and Wiltschko, 2005; Mouritsen, 2018), though the anatomical location and mechanism of the putative magnetoreceptors themselves remains controversial. The most widely supported magnetoreception mechanism, however, involves a light-dependent sensor in birds' eyes (Hein *et al.*, 2010; Hore and Mouritsen, 2016). Consequently, it is thought that birds should fail to orientate correctly in complete darkness. High levels of light might also render the magnetic compass ineffective, since it appears to be primed by very low light intensities of 3×10^{-4} lux – a theory supported by the observation that free flying birds are capable of orienting towards their migratory direction even during dark moonless nights (Cochran, Mouritsen and Wikelski, 2004). Nevertheless, it has been suggested that under rainy and cloudy conditions, there is not enough natural light, so birds congregate around lit up areas, seeking places where their magnetic sense works correctly ('Magnetoreception-seeking theory' in Evans *et al.*, 2007). Furthermore, the studies showed that under higher light intensities of monochromatic red colour the orientation of birds becomes random, suggesting that the sensory mechanism of magnetoreception fails to work correctly (Muheim, Bäckman and Åkesson, 2002). Thus, it has been proposed that red light of broadcasting towers might oversaturate the mechanism of magnetoreception, resulting in birds being disoriented (‘Magnetoreception disruption theory’ in Evans *et al.*, 2007).

Procellariiformes are not reported to congregate in areas with red light. Salamolard *et al.* (2001) found that they are attracted to blue and green rather than red light. Thus, it is unlikely that seabirds’ magnetic sense is disturbed by light pollution resulting in their grounding, but they might be seeking the geomagnetic engagement by arriving at lit-up areas. Despite numerous studies, there is no evidence, however, for the use of a magnetic compass in seabirds (Massa *et al.*, 1991; Benhamou *et al.*, 2003; Benhamou, Bonadonna and Jouventin, 2003; Bonadonna *et al.*, 2003, 2005; Mouritsen, 2003; Pollonara *et al.*, 2015; Padget *et al.*, 2017). Past studies focused on disturbing behaviour of foraging adult birds. A magnetic compass, however, remains a likely candidate at least for movement control that is necessarily inherited i.e. first-time migration of a juvenile seabird without adults (Liedvogel, Åkesson and Bensch, 2011). Thus, further research should check if young inexperienced birds are good candidates for finding evidence of magnetoreception in seabirds.

Visually mediated light pollution effects

A simpler explanation of birds' reaction to the different spectra and intensities of light would be interspecific differences in the visual perception of birds. Avian species differ in spectral sensitivity, consequently perceiving colours with different intensities (Varela, Palacios and Goldsmith, 1993). Thus, some species are able to perceive some spectra of light from further away than others, which might result in greater attraction to light. These interspecific differences could explain various reaction of birds that are either attracted to red or blue wavelengths (Gautereaux and Belser, 1999; Evans *et al.*, 2007). Moreover, Salamolard *et al.* (2001) reported that the groundings of Tropical shearwaters (*Puffinus bailloni*) are reduced in red rather than blue and green light, which is consistent with the high likelihood that, as diving foragers, shearwaters are more sensitive to blue light (Hart, 2004).

There are several ways in which seabird vision could be affected by light pollution and result in grounding. These potential mechanisms fit into our framework of primary and secondary influences of light pollution on seabirds' navigational mechanisms. Secondary influences could result from a connection between light and food, and two mechanisms could explain this relationship. First, some of the prey targeted by Procellariiformes is bioluminescent, such as squids, lanternfish and lightfish (Imber, 1976). Young and inexperienced fledglings might mistake streetlights for the light of a prey and thus be drawn towards light pollution (Imber, 1975). This would however not explain the behaviour in all species, like for example Manx shearwaters which do not forage at night (Shoji *et al.*, 2016). Second, a seabird nestling sees only light streaming in from the burrow entrance for the first months of its life. Parents arrive via the entrance bringing a meal for the nestling; thus, an association between food and light coming from the entrance could be formed (proposed in Rodríguez *et al.*, 2017). However, if seabirds misinterpret light as indicating food, we would expect them to crash directly into light sources. Instead seabirds collide mainly with structures such as walls, trees, or the ground (personal observations). Thus, it is unlikely that seabird's orientation towards light is caused by secondary influences.

A primary influence of light on the orientation of seabirds can be explained by artificial lights disturbing the correct appearance of celestial objects, resulting in seabirds being unable to use them as cues. Alternatively, seabirds could erroneously utilise the ALAN as a navigational cue (Telfer *et al.*, 1987). The fact that fewer grounded seabirds are observed during full moon (Miles *et al.*, 2010) supports this theory, as artificial light would be less prominent relative to moonlight. It would not, however, explain the bias towards juveniles seen in grounded seabirds (Rodríguez *et al.*, 2017). I would like to propose another way in which the primary influence of light could result in seabirds grounding. Seabirds might behave like hatchling marine turtles. As described above, after emerging from the nest, turtles crawl towards the lowest, brightest point on the horizon (Kamrowski *et al.*, 2014). A similar behaviour in nocturnally fledging seabirds might normally ensure that the young fly away from land and towards the sea. Light pollution, however, might incorrectly redirect their orientation towards the land. Even if, seabirds leave the lit-up area, suggested mechanism would result in a bird coming back to the light sources and circling around them. Eventually, exhausted bird might land on the ground. This explanation is further supported by the fact that adult turtles are not attracted towards light pollution (Silva *et al.*, 2017). This discrepancy in behaviour towards the light in both groups of animals has been explained by difference in developmental stage of their eye (Atchoi, Mitkus and Rodríguez, 2020).

As presented above, there might be many ways for light to cause misorientation or disorientation in Procellariiformes and result in their grounding in cities and towns. The aim of my D.Phil. thesis is to investigate the drivers of grounding behaviour in Procellariiform seabirds, using Manx shearwaters as a model species, and to give new insight into the influence of light pollution on their orientation.

Why is it important to understand seabird grounding?

Seabirds, as long-lived marine top predators, are used as indicators of marine condition globally and regionally (e.g. Camphuysen, 2006; Piatt, Sydeman and Wiese, 2007; Parsons *et al.*, 2008). Yet, seabirds are also the most endangered group of birds on the earth, with the order Procellariiformes having the highest proportion of threatened species (Paleczny *et al.*, 2015; Dias *et al.*, 2019). Rodríguez *et al.* (2019) ranked the threats posed to threatened pelagic seabirds in order of priority and ‘light pollution’ came second after ‘invasive alien species’. Other threats include climate change, habitat loss, human exploitation, overfishing, marine pollution and bycatch (Rodríguez *et al.*, 2019). The wide-ranging distribution of seabirds across the world’s oceans and their extraordinary migrations cross many jurisdictions and high seas, make it a real challenge to set correct aims and boundaries for conservation areas. Of threats seabirds face however, light pollution, second on the priority list, might be a relatively straightforward issue to address as it is spatially constrained and could require simpler mitigations measures than other threats. Understanding the drivers of light-induced seabird groundings is therefore both important to inform conservation mitigation and likely to provide tangible conservation impact.

Such knowledge is urgently needed as twenty-four seabird species affected by ALAN are threatened and there are documented reports of population declines attributed to artificial light (Day, Cooper and Telfer, 2003; Fontaine, Gimenez and Bried, 2011; Rodríguez, Rodríguez and Lucas, 2012). In Tenerife only, up to nine different species of seabirds are affected by artificial light (Rodríguez and Rodríguez, 2009), while more than 30 000 birds were rescued on the island of Haui in Hawaii over 30 years of rescue (Ainley *et al.*, 2001). Light pollution affects Procellariiformes in coastal areas but also at sea near boats and oil platforms (Ryan, 1991; Wiese *et al.*, 2001; Black, 2005; Merkel and Johansen, 2011; Glass and Ryan, 2013; Day *et al.*, 2015; Ronconi, Allard and Taylor, 2015).

Correctly quantifying the real threat of light pollution to seabirds is difficult, as most of the reports are based on volunteering efforts and documenting mortality at sea has proved to be challenging (Montevecchi, 2006; Rodriguez *et al.*, 2017). Thus, current assessments probably represent an underestimate. With > 40% of the world's human population living in coastal areas (Small and Nicholls, 2003), and the ever-growing, unconstrained use of ALAN, the threat to seabirds posed by light is very likely to expand, so it is important that a correct understanding of the issues must guide remedial and mitigation actions.

The Manx shearwater

My study species, the Manx shearwater (*Puffinus puffinus*), is a medium seabird (~400g, Fig 1.1A) which flies thousands of kilometres every year by staying close to the sea surface and using dynamic soaring for efficient travel (Paiva *et al.*, 2010; Spivey, Stansfield and Bishop, 2014; Tarroux *et al.*, 2016; Ventura *et al.*, 2020). Manx shearwaters are listed as "least concern" by the IUCN with a global population estimated to be around 790,000 mature individuals (BirdLife International, 2018). Their breeding grounds are distributed around the North-East Atlantic and particularly in Great-Britain and Ireland. The biggest colony of ~317,000 breeding pairs is located on Skomer Island, Wales (Perrins *et al.*, 2012), where most of the experiments reported in this thesis were undertaken. The rest of the population is mainly congregated on three other islands in the UK (Skokholm, Rum and Lighthouse Island in the Copeland archipelago), but there are smaller colonies in Ireland, Iceland, France, the Canary islands and in the Azores, as well as a few very small colonies in North America (BirdLife International, 2018).

Manx shearwaters are mainly active at sea during daylight and twilight hours (Shoji *et al.*, 2016), but visit their burrows only at night, possibly to avoid diurnal predators such as the great black-backed gull (*Larus marinus*; Watanuki, 1986; Keitt, Tershy and Croll, 2004; Silva *et al.*, 2011). The breeding season starts in April, when most of the birds found in a colony are males defending their burrows (Brooke, 1990). Females, in the meantime, having visited the colony early on, embark on a ~2-week pre-laying exodus journey, often far out to sea (Dean, 2012), during which time they build a single large egg (~15% of body mass). Shearwaters form long-term monogamous pairs and cooperate to incubate an egg for ~ 51 days and then, after hatching, alternate chick feeding visits to the colony over next ~ 60 days (Tyson *et al.*, 2017). The nest of a Manx shearwater is located in a burrow, so after the chick has hatched (Fig. 1.1B) and grown over the first few days of its life, it is left alone by its parents safely underground. In the few days before fledging, the young go out on the surface at night to exercise their wings and eventually fledge, starting a long-distance trans-equatorial migration. It is not well known where juvenile and immature Manx shearwaters spend their first few years at sea, but evidence from ringing recoveries suggest that they embark on a similar migration to adults, flying to the Patagonian shelf along the Argentinian coast (Brooke, 1990; Guilford *et al.*, 2009; Freeman *et al.*, 2013).

Fledgling Manx shearwaters, like other Procellariiformes*,* are reported to ground due to light pollution near their nesting sites. Volunteers in Tenerife (Rodríguez *et al.*, 2008), Scotland (St. Kilda - Miles *et al.* (2010); Mallaig - Syposz *et al.* (2018)), and around the mainland coast of Wales, near Skomer and Skokholm Islands (Anna Sutcliffe pers. comm.) rescue young Manx shearwaters and release them back to the sea (Fig. 1.1C,D).

So far, the number of Manx shearwaters killed due to ALAN was reported as negligible in proportion to the global population (Carboneras, Jutglar and Kirwan, 2014). Other threats include habitat destruction, human exploitation in the form of legal harvesting (for example, on the Faroes of 1,000–5,000 chicks per year: Thorup *et al.*, 2014), entanglement in fishing gear (Žydelis *et al.*, 2009), oil spills (Votier *et al.*, 2005), and other types of marine pollution (Camphuysen, Schouten and Gronert, 2010). The introduction of invasive species has also been a problem for this species, with the most notable example from the Calf of Man where the whole colony, estimated to be the largest in the world, became extinct due to an accidental introduction of rats after a shipwreck in the 18th century (Brooke, 1990). Therefore, despite the fact that the population of Manx shearwaters is relatively large, and the threats are thought to be modest, like other Procellariiformes, Manx shearwaters are inherently vulnerable owing to breeding in large numbers on relatively few, dense colonies, which are extremely vulnerable to the introduction of ground predators. This highlights the importance of setting necessary precautions to ensure that the colonies remain safe havens for the species.

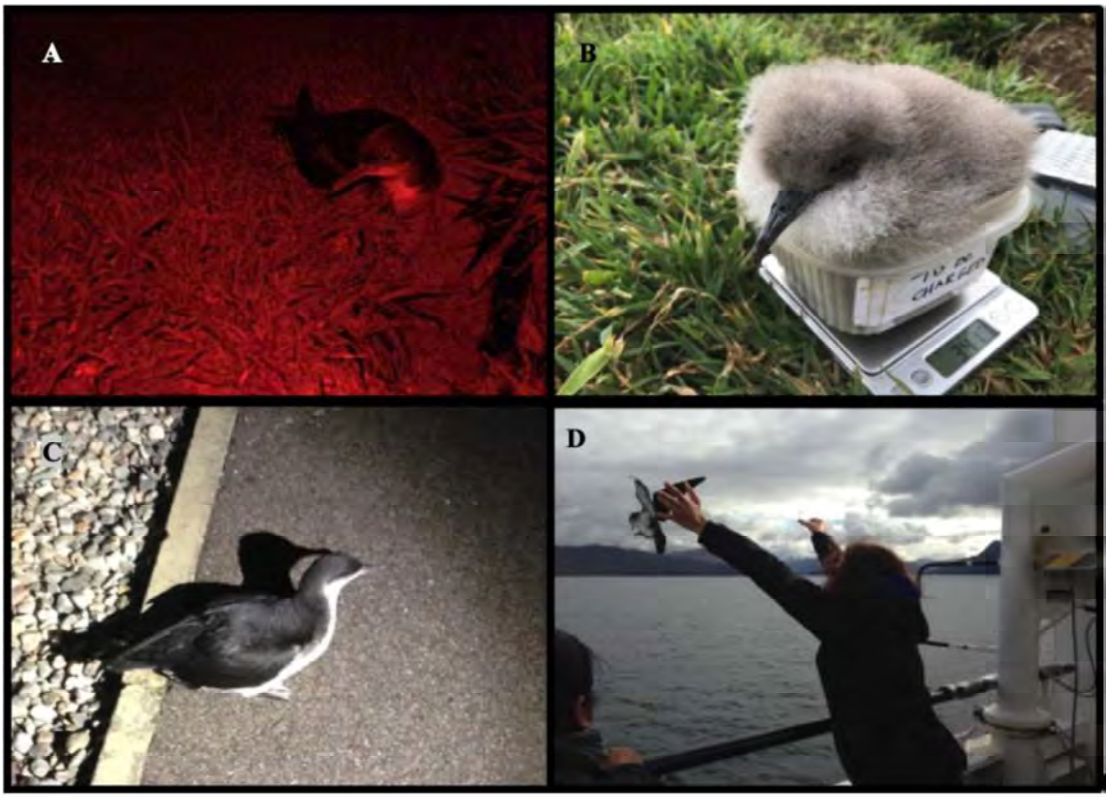

Figure 1.1 (**A**) A Manx shearwater at the colony. (**B**) A Manx shearwater juvenile being weighed for research purposes. (**C**) A grounded Manx shearwater in Mallaig, Scotland. (**D**) A volunteer releasing a rescued Manx shearwater back to the sea.

Objectives and structure of the thesis

The aim of this thesis is to investigate how light pollution affects the orientation of Procellariiform seabirds by combining novel experiments with observations of adult and juvenile Manx shearwaters. It is comprised of four research chapters, all of which are written in manuscript format and as stand-alone research papers. Each chapter contains an introduction relevant to the set of questions it tests.

Chapter 2 presents the first experimental study of light pollution in Manx shearwaters and investigates the influence of the duration, colour and intensity of light on the nocturnal flight behaviour of adult Manx shearwaters by recording flying birds using a thermal video camera.

In **Chapter 3**, I look for evidence of magnetoreception in juvenile Manx shearwaters. Magnetoreception in juvenile seabirds has been proposed as a potential mechanism that could be disturbed by light pollution (Evans *et al.*, 2007) and thus could cause groundings in Procellariiformes. Our study assesses the use of a magnetic compass in juvenile Manx shearwaters by attaching a strong magnet to the birds' head and observing their orientation during fledging. I further test the influence of the wind and topography on their initial orientation.

In **Chapter 4,** I follow on previous observations of migratory orientation of juvenile Manx shearwaters, and undertake a study looking into their initial orientation on the ground. I describe a novel assay that allows observing initial orientation of seabirds and test if the orientation is affected by various variables, including artificial light pollution.

Chapter 5 takes a more applied approach and investigates ten years of data on groundings collected by citizens in a village in Scotland where numerous Manx shearwater fledglings ground every year. The streetlights in the village recently changed from high and low sodium pressure to LED bulbs. I investigate whether this transition changed the light intensity around the village and whether it had an effect on the number of grounded Manx shearwaters.

Finally, in **Chapter 6** I summarise and discuss my main findings together and their potential applications for other fields such as conservation, and I conclude with future directions for this work.

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Chapter 2

Avoidance of adult Manx shearwaters to different durations, colours and intensities of light pollution.

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ABSTRACT

With increasing evidence for effects of artificial light at night (ALAN) on the physiology and behaviour of wild animals, conservation concerns about its effects on wildlife are rising. One of the profound ways in which ALAN may affect animals is by influencing their movement. Among birds, Procellariiform seabirds are often found grounded in areas polluted by light and struggle to take to the sea again without human intervention. Hence, understanding their general responses to different wavelengths and intensities of light is urgently needed to inform mitigation measures. Here, we investigate how colour and intensity of light affect the nocturnal flight behaviour of Manx shearwaters *Puffinus puffinus*.

We experimentally introduced lights of different colour and intensities at a dense colony of Manx shearwaters. The density of birds in flight above the colony in the vicinity of the light during the 'on' and 'off' phases was measured using a thermal imaging camera. Contrary to our expectation, we observed fewer shearwaters in flight during light-on periods, suggesting that these adult shearwaters were repelled by the light. This effect was stronger with higher intensities and increasing duration of light-on pulses, and with short wavelength (green and blue) compared to long wavelength (red) light.

Our findings show how some seabirds respond to different characteristics of light pollution. Current guidelines for reducing light pollution have focused on places where seabirds ground. Our evidence suggests that these mitigation measures should be also implemented at breeding colonies and in their vicinity.

INTRODUCTION

Artificial light at night (ALAN) may be installed for the purpose of warning of potential obstructions in otherwise dark environments, for instance lighthouses, navigation buoys, or aircraft warning lights on pylons and tall buildings. Other artificial lights provide better visibility, entertainment, an enriched aesthetical value of structures and safety on the streets for humans (Beyer and Ker, 2009; Kyba *et al.*, 2018). Many artificial lights are, however, often detrimental to humans' health (Cho *et al.*, 2015; Kumar *et al.*, 2019), negatively affects the physiology and behaviour of wildlife (Da Silva et al., 2015; Dominoni et al., 2013; Gaston et al., 2013; Rich and Longcore, 2013), and can impact interactions between species (Frank, 1988; Kuijper et al., 2008). The effects of light pollution on the environment are broad, and mounting evidence indicates a wide range of impacted species, of which many are yet to be documented.

One of the profound ways in which light pollution may affect individual animals is by altering their movement. Effects of light pollution on animal movement can manifest either as attraction to light (positive phototaxis) or repulsion from light (negative phototaxis). Negative phototaxis in response to ALAN has been observed across numerous taxa, including nocturnal bats, spiders, insects, mountain lions, and migratory birds, with consequent costs for their health and survival when their patterns of movement are restricted or forced to change (Beier, 1995; Nakamura and Yamashita, 1997; Summers, 1997; Kuijper *et al.*, 2008; Cabrera-Cruz *et al.*, 2020). Such behavioural alterations can exacerbate existing negative forces, such as habitat fragmentation, thus having adverse impacts at individual and population levels and causing conservation concern. In addition to the problem posed by repulsion from light, positive phototaxis can also negatively impact animal populations, for example by causing fatal collisions with light emitting objects (e.g. streetlamps, buildings, radio towers) or entrapment in artificially lit areas. Such areas may either lack resources or have a higher exposure to predators (Perry, Buchanan and Fisher, 2008; Rodríguez *et al.*, 2017; Owens and Lewis, 2018; P. Wilson *et al.*, 2018).

Attraction to light is especially common in birds, causing thousands of casualties annually due to collisions with illuminated structures, including lighthouses (Squires and Hanson, 1918), broadcast towers (Ogden, 1996), wind turbines (Kerlinger *et al.*, 2010) and buildings in towns (Rodríguez *et al.*, 2017). Interestingly, and of relevance to potential mitigation measures, the extent of the attraction to ALAN has been found to vary with the duration, intensity and spectrum of the light (Baldwin, 1965; Gautereaux and Belser, 1999; Jones and Francis, 2003; Evans *et al.*, 2007). Lowering the intensity and duration of light results in a decrease in number of affected birds across different study sites (Tufts, 1928; Baldwin, 1965; Avery, Springer and Cassel, 1976; Reed, Sincock and Hailman, 1985; Verheijen, 1985; Jones and Francis, 2003; Rodríguez *et al.*, 2014). The reaction of birds to the wavelength of light, however, is equivocal. Studies variously recommend either broadband white light (Gautereaux and Belser, 1999) or long wavelengths (red and yellow, Evans et al., 2007; Salamolard et al., 2001; Zhao et al., 2020) for reducing attraction in birds. These contrasting findings might be caused by interspecific differences in spectral sensitivity. Thus, in order to determine which light wavelengths minimise attraction for the relevant species, a taxon-specific approach has been recommended (Rodríguez *et al.*, 2017).

Although many birds are affected by light pollution, the species most regularly found to land in lit areas—a phenomenon known as “fallout” or “grounding”—are nocturnal seabirds, Procellariiform in particular (Telfer *et al.*, 1987; Troy, Holmes and Green, 2011). These birds cannot easily become airborne from a built-up area due to their anatomy, which is adapted to life at sea (Warham, 1977). They require a slope, a gust of wind or a long runway to take-off, but cars and buildings form a barrier, and so groundings can often be fatal (Rodríguez *et al.*, 2012, 2014). There has been little investigation into the response of Procellariiformes to different wavelengths of light, and so far our knowledge is limited to evidence for greater attraction to blue and green colours than red and yellow in Tropical shearwaters (*Puffinus bailloni*; Salamolard et al., 2001). These findings are supported by an examination of the retina of wedge-tailed shearwater (*Puffinus pacificus*), which revealed physiology that indicates that they are more sensitive to short (blue and green) wavelengths of light than to longer-wavelengths (red; Hart, 2004). Further investigation is therefore required to obtain a better understanding of the impact of different wavelengths on Procellariiform seabirds. In addition, most studies have focused on the effect of light pollution in urban areas where birds ground, but light pollution also occurs at or near breeding grounds and how this may affect behaviour remains unknown.

Here we aimed to investigate the relative effects of the duration, colour and intensity of light on the flight behaviour of a Procellariiform seabird at the breeding colony with a novel experiment combining light exposures of varying characteristics. We monitored birds with thermal imaging, which allowed us to study how the flight behaviour of adult Manx shearwaters (*Puffinus puffinus*) was affected by different lighting characteristics during nocturnal visits to the colony without causing additional light disturbance. We counted the number of shearwaters in the field of view of the thermal camera while varying the intensity and the spectral wavelength of light at the colony (experiment 1), or while varying the intensity and duration of flashes of white light at the colony (experiment 2). Assuming that light affects adult shearwaters at the breeding colony in a manner similar to those reported by studies looking at passerines and juvenile seabirds (Tufts, 1928; Baldwin, 1965; Avery, Springer and Cassel, 1976; Reed, Sincock and Hailman, 1985; Verheijen, 1985; Jones and Francis, 2003; Rodríguez *et al.*, 2014), we expected that more birds would be observed with increasing duration and intensity of light (positive phototaxis). Furthermore, we expected to find a decrease in the number of birds counted — i.e. a lower attraction — with increasing wavelength, following observations of greater sensitivity to a lower wavelength in two closely related species (Salamolard *et al.*, 2001; Hart, 2004).

METHODS

Site and species

The Manx shearwater (*Puffinus puffinus*) is a medium-sized seabird from the order Procellariiformes which breeds on islands in the North Atlantic between April and September. Similar to many other Procellariiformes, the nests of Manx shearwaters are located in underground burrows and adults visit them only during the night, probably to avoid predation (Watanuki, 1986; Keitt, Tershy and Croll, 2004; Silva *et al.*, 2011). In autumn, young birds fledge at night and this is when they are particularly susceptible to the impacts of ALAN. Manx shearwater groundings are reported frequently close to colonies on Tenerife (Rodríguez *et al.*, 2008), in western Scotland (Miles *et al.*, 2010; Syposz *et al.*, 2018), and around the mainland coast of southwest Wales, near large colonies of shearwaters located on Skomer and Skokholm Islands, Pembrokeshire (Anna Sutcliffe pers. comm.).

Skomer Island (Pembrokeshire, southwest Wales, UK., 51° 44’ N, 5° 17’ W, Fig. 2.1), where this study was undertaken, hosts the biggest colony of Manx shearwaters in the world, of around 317,000 breeding pairs (Perrins *et al.*, 2012). There is some anthropogenic light from vessels and the costal developments 5km away from Skomer Island, but there is very little anthropogenic light on the island itself, with a maximum of ~30 people staying on the island overnight. At night, staff and tourists use dim red lights or red filters on their torches.

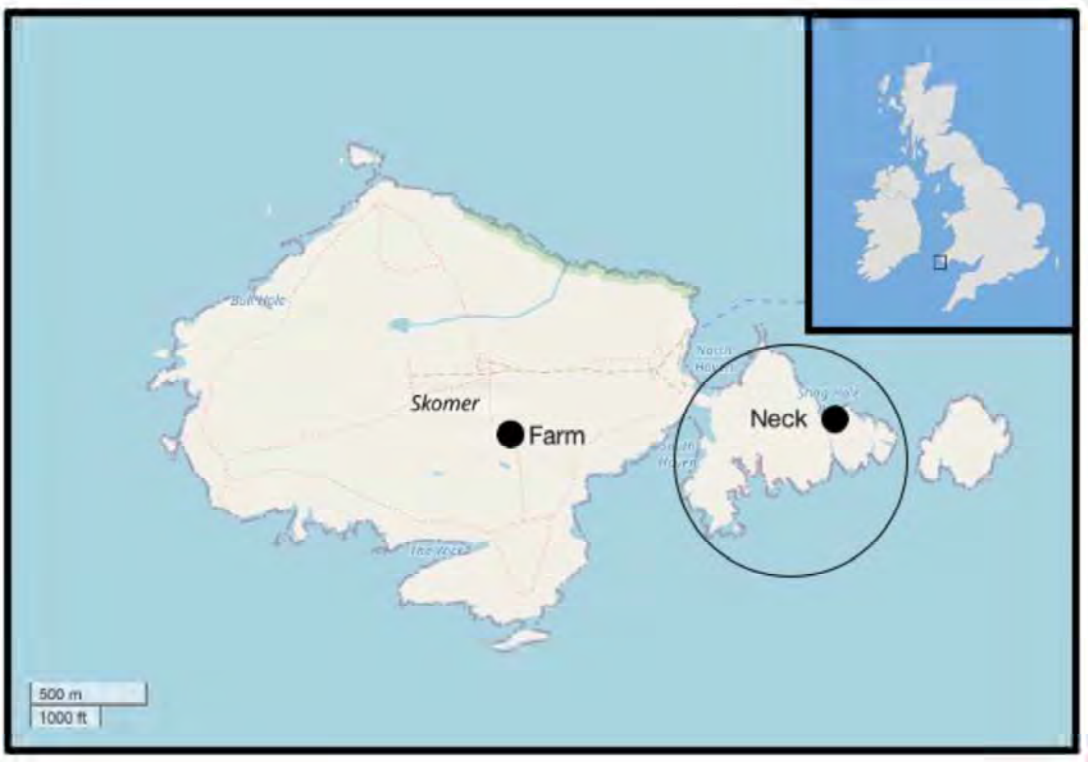

Figure 2.1. Map of Skomer Island. It shows the locations of the experiment on the Neck (right) and near to the farmhouse (the Farm, left) indicated by black dots. The area that tourists are not allowed to access is encircled in black (OpenStreetMap®, 2020).

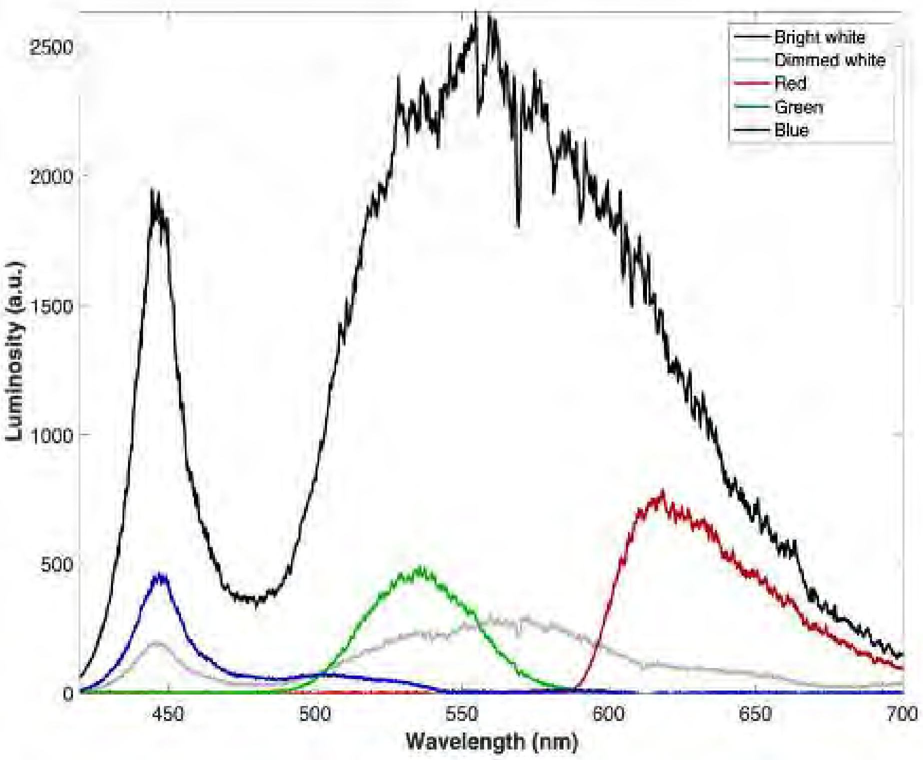

Figure 2.2. Spectrum of the light sources. Wavelength-dependent intensity of the light source employed depending on the filter in place to produce the light sources required; namely red, green, blue, dimmed white, and bright white. The spectra were measured using an OceanOptics USB2000+ fibre optic spectrometer, which was calibrated using an Oriel Instruments 6035 Hg (Ar) lamp. With the filters in place, it was found that that the central wavelength and bandwidths (Full-Width-At-Half-Maximum) when using the filters were 450nm (18nm), 540nm (45nm), and 620nm (60nm) for the blue, green, and red filters, respectively. The total measured signal can be integrated to get an estimate of the radiant flux for each source. The flux for the source (bright white) was 32W, whereas the flux was found to be 3.3W for the dimmed white, 4.3W using the red filter, 2.0W using the green filter, and 1.4W using the blue filter. Therefore, by using the filters, the total brightness of each light source was of the same order of magnitude, with an average value of (2.7±1.3) W.

Experimental design

The experiment was undertaken over 21 days, between 14th June and 14th August 2018. A Forward-Looking Infrared thermal camera (FLIR T620, Axsys Technologies, Rocky Hill, Connecticut, United States) with frame rate of 18.84-20.6Hz was used to record the flight behaviour of Manx shearwaters during the experiment. Next to the camera, a T50 Waterproof LED Torch (Icefire Lighting Ltd., Shen Zhen, China), similar to those used regularly by the staff and visitors, was positioned and covered with gel filters (Cokin®, Rungis, France) to achieve different colours (Fig. 2.2, Table S2.1). Due to the sensitivity of the thermal camera, the study was undertaken only on days with no or little rain. All work was conducted after ethical approval by Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford's Local Ethical Review Process.

The study consisted of two experiments designed to investigate the influence of light on the behaviour of shearwaters. The first assessed the effect of different spectra and intensities of light, whereas the second investigated the influence of different lighting intervals and light intensities. For both experiments, we recorded footage of shearwaters in flight in front of the camera throughout the experiment for later analysis.

The spectra experiment: This experiment used different spectra of light - blue, green and red - of similar intensity (Fig. 2.2). We also used broadband white of similar intensity ('dimmed white') and a tenfold more intense broadband white ('bright white'). The experiment was split into 'control' and 'experimental' pairs which comprised two 1-minute intervals (Fig. 2.3A). The design included the control pair, as it allowed for comparing the effect of different colours between each other. For control pairs, the light was kept off for both 1-minute intervals, while for experimental pairs the light was switched on for the first minute, then off the second. This resulted in two explanatory variables: light (‘on’ and ‘off’) and torch setting (‘blue’, ‘green’, ‘red’, ‘dimmed white’, ‘bright white’ and ‘control’). The order in which control and experimental pairs were arranged was selected each day using a constrained randomised design: each of the six pairs was used 10 times over two hours, and none of the settings was repeated more than two times in a row.

The experiment was undertaken at two locations on Skomer Island: first, near to the farmhouse, regularly disturbed by the presence of tourists, and second, on the Neck, an area that is not accessible to tourists (Fig. 2.1). To control for night brightness, we used a Sky Quality Meter (SQM, Geoptik, Verona, Italy) to measure ambient light levels in magnitudes per square arc second (mag arcs^{-2}). Night brightness for each hour of the experiment was taken to be the mean between measurements taken at the beginning and at the end of the hour. The night brightness was then rescaled so that 0 was the mean.

The interval experiment: This experiment involved turning on two intensities of broadband white: ‘dimmed white’ and a tenfold more intense ‘bright white’ for 1-, 10- and 20-minute intervals (Fig. 2.5A). We used a similar pairing structure for our treatments as in the spectra experiment, in which treatment pairs comprised two consecutive intervals of equal duration (1-, 10- or 20 minutes). In control pairs, the light was kept off for both intervals. In experimental pairs, the light was switched on for the first interval, and switched off for the second. This resulted in three explanatory variables:

interval duration (1, 10, 20min), torch setting ('dimmed white', 'bright white' and 'control') and light ('on' and 'off'). The order of experimental and control pairs was selected every day using a constrained randomised design in R (version 1.1.456, R Core Team 2018); each of the six combinations (setting x interval) was used once over a night. Due to time constraints the interval experiment was limited to one location (the Neck) and days with no moon.

Data analysis

We counted the number of birds in flight in the videos using the Motion-Based Multiple Object Tracking module in MATLAB (R2017a, MathWorks Inc.) which tracks moving objects in two-dimensions. The parameters were set to track objects bigger than 20 pixels and smaller than 4000 pixels. This threshold was set to only recognise birds that were minimum 5m away and maximum 85m away from the camera (Fig. S1.2). To validate the method, birds were manually counted in 5-minute samples of each c.1-hour video that was run through the software, for a total 4 hours out of the 47 hours 28 minutes of footage. We sampled different light regimes to account for any biases.

Analyses were conducted in `R` (version 1.1.456, R Core Team 2018). The package '`mgcv`' (Wood, 2011) was used to construct generalised additive models (GAMs) with log link and negative binomial error distributions. The model assessed whether the number of birds differed between treatments while accounting for fluctuations in the colony attendance of shearwaters over the nights of the experiment.

The spectra experiment: We fitted a model with the following formula to the data:

Birds_count ~ Torch_Setting * Light * Location +
Torch_Setting * Light * Night_Brightness +
(random = Pair) + (random = Day) + s(Time)

In this model, the response continuous variable was the number of counted birds per 1 minute and the categorical explanatory variables of torch setting, on/off light a location (the Neck/the Farm) and the continuous variable of night brightness. We included the smoothed term (thin plate regression splines with basis dimension chosen automatically) of time relative to midnight ('Time') to account for non-linear variation in bird densities throughout the night which was unrelated to treatment (e.g. due to weather factors and the birds' regular circadian patterns). This variable additionally served to account for temporal autocorrelation. Julian date ('Day') was included as a random term to account for any changes caused by differences in weather between days. Additionally, a variable "Pair" was included as a random term in the model to reflect the paired design of the experiment. "Pair" assigned a consecutive number to each experimental and control pair. Since our independent variable was counts of flying birds, we initially used a Poisson error distribution, but the model showed significant overdispersion and therefore a Negative Binomial model was used instead (sum of squares of residuals/residual degrees of freedom, Poisson = 2.79, Negative Binomial = 1.16).

We then tested our hypotheses using post-hoc contrasts designed with the '`emmeans`' package (Lenth *et al.*, 2018). Specifically, we designed post-hoc test to compare the difference in bird count between the two parts of the experimental pair ('on' vs. 'off') with the control pair difference (‘off’ vs. ‘off’), as well as between experimental pairs. In essence, we compared a difference in counted birds of each experimental pair (e.g. blue light vs. light off) with a control pair (light off vs. light off) and other experimental pairs (e.g. red light vs. light off). We also tested whether location had an effect on the difference in experimental pairs of the same torch setting (e.g. green light vs. light off on the Neck comparing to green light vs. light off at the Farm) and if night brightness had an effect on the difference in experimental pairs comparing to control pairs. All the p values were adjusted with a Tukey correction for multiple post hoc testing.

The interval experiment: We analysed the interval experiment using GAMs with a log link and Negative Binomial error distributions. Similar to the spectra model, the Poisson error distribution caused overdispersion in the model, so we used a Negative Binomial distribution instead (sum of squares of residuals/residual degrees of freedom, Poisson =3.49, Negative Binomial =1.02). This time we fitted a model with the following formula to the data:

Mean_of_birds_count ~ Torch_Setting * Light * Interval_Time +

(random = Pair) + (random = Day) + s(Time)

In this model, the response variable was an average of counted birds per minute across the interval. The explanatory variables were three categorical factors of torch setting, on/off light and the interval time (1min, 10min, 20min). Similar to the spectra experiment, we used a smooth term of the time relative to midnight, and random terms of “pair” and Julian date.

The ‘`emmeans`’ package was used to compare differences in experimental pairs to the control pairs in each interval time separately. In essence, we compared the difference in the average of counted birds in each experimental pair (e.g. bright white 10min vs 10min light off) with a control pair (e.g. 10min light off vs 10min light off). All the p values were adjusted with a Tukey correction for multiple post hoc testing.

RESULTS

The collection of the data resulted in 47 h 28 min of the video (17 h 30 min for the spectral experiment and 29 h 58 min for the interval experiment). Validation of the Motion-Based Multiple Object Tracking module showed that counts of birds performed by the module (supervised machine learning) and those counted manually were well correlated (Pearson's Correlation test sample estimates 96.72% ± 0.93%, $t_{238} = 58.791$, $p < 0.001$, Fig. S2.2). Thus, we used the counts obtained through machine learning as the experimental measurement throughout all the video sequences (including those sections of video used as test periods for manual selection). This choice produced an objective, reproducible and reportable method of measurement without any bias through human intervention in selection.

The spectra experiment: Our GAM for the spectra experiment was well fitted with 92.9% of deviance explained. Exposure to all colours except red resulted in a significantly lower count of birds than in control (light off) periods (Table 2.1, Fig. 2.3B, Fig. 2.4). Bright white had the strongest effect, causing a 33% (95% CI [24, 40]) reduction in counted birds compared to the control pair ('off', 'off'). Dimmed white, blue and green colours weren't significantly different from each other, causing a similar effect (decreases of 18% (95% CI [8, 27]), 19.1 % [9, 28], and 19.6% [10, 28], respectively). Exposure to red light had no significant effect on the number of flying birds and this treatment was significantly different from all the others (Table 2.1).

Birds reacted similarly to the light treatments both on the Neck and at the Farm (Table 2.2). For the red light treatment only, we observed an effect of the ambient brightness on a given night on the numbers of observed shearwaters (Table 2.3): for every 1-unit increase (representing one standard deviation), there was a 22.2 % (95% CI [6, 35]) increase in the difference between red light on and off. In other words, the effect of red light was most evident during dark nights comparing to moonlit nights (Table 2.3). The rescaled SQM measurement varied between -1.3 (bright night) to 1.25 (dark night). The smoothed terms of time relative to midnight, as well as the random effects of 'pair' (paired on/off lights) and calendar day showed significant effects on the numbers of birds counted, implying that there was variation owing to other aspects of the birds' seasonal biology and daily routines, which we accounted for in our model (Table S2.2).

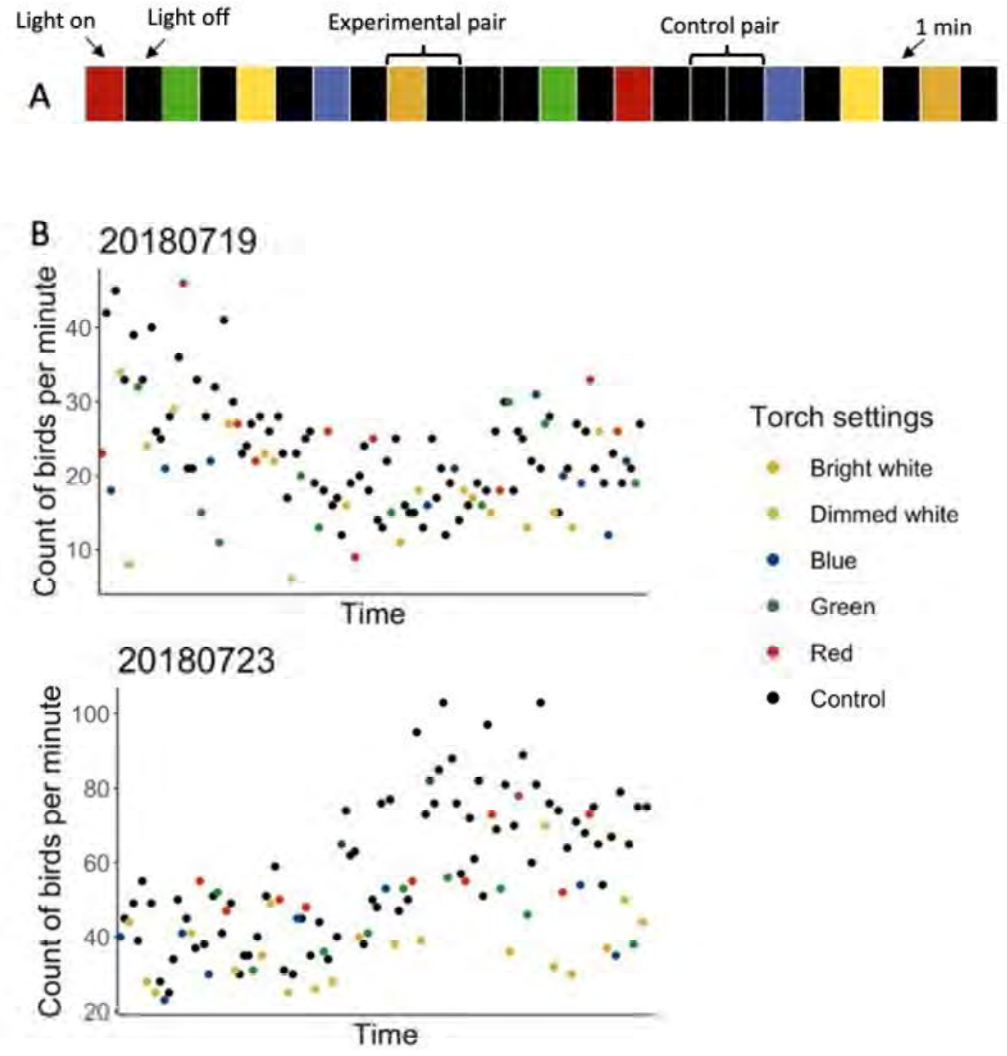

Figure 2.3. (A) Visualisation of an example of treatment series of the spectra experiment. We turned the torch on for 1min and off for 1min. Each experimental pair (‘on’, ‘off’) has a colourful segment corresponding to one of five different settings (‘red’, ‘green’, ‘blue’, ‘dimmed white’ and ‘bright white’) and black segments showing the light off. Two black segments indicate a control pair (‘off’, ‘off’). **(B)** Two example days of the spectra experiment undertaken at the Farm (19th July 2018 starting at 23:40BST) and on the Neck (23rd July 2018 at 00:07BST). They show the count of birds per minute against the time. Different colours of the dots represent various torch settings.

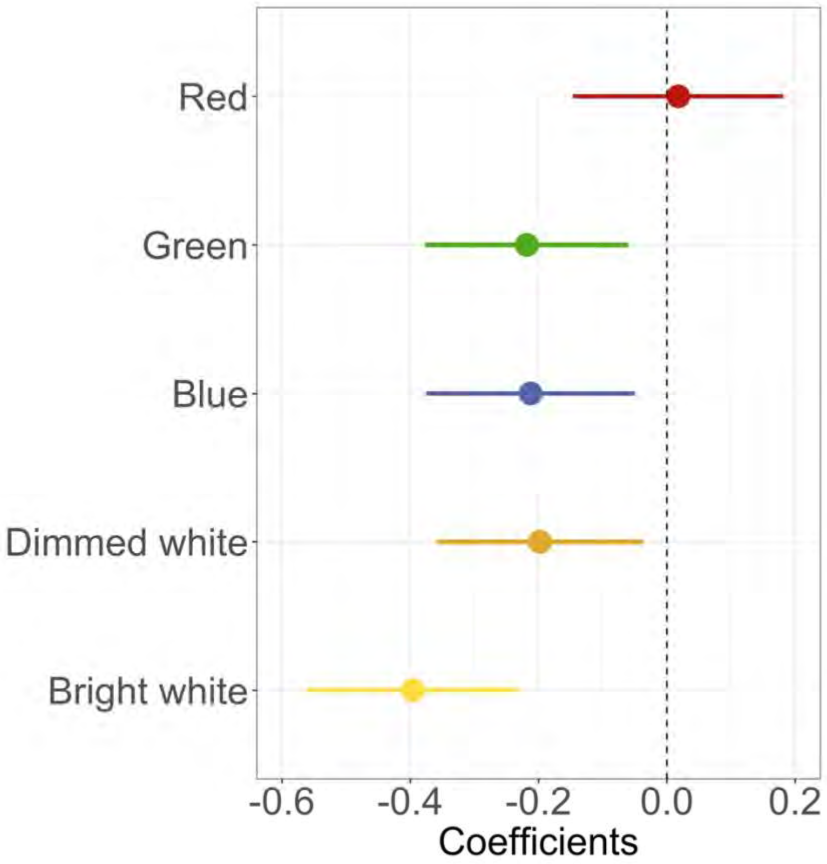

Figure 2.4 The graph represents the results of post-hoc test in the spectra experiment. It shows the coefficients of five experimental pairs when comparing the difference in light on vs light off to the control (light off vs light off, dashed vertical line). All the colours except red had a significant influence on bird counts, with lower numbers of birds when the light was on. For detailed statistics, see Table 1.1.

Table 2.1. Summary of the results of post-hoc pairwise tests of the comparison of differences in between experimental pairs (‘on’, ’off’) and comparing to control pair (‘off’, ‘off’). Negative coefficients indicate that bird numbers decreased in the presence of illumination compared to control periods. Estimates taken from GAM (spectra experiment) show log-transformed differences in counted birds. For example, bright white caused a (0.67 – 1) * 100% = -33% decrease in counted birds when we turned on the light compared to control pair (‘off’, ‘off’). ***P < 0.001; **P < 0.01; *P < 0.05.

Comparisons	Estimate	Odds Ratio	Std. Error	t ratio	p-value
Control vs Bright white	-0.396	0.673	0.06	-6.58	<0.0001 ***
Control vs Dimmed white	-0.198	0.82	0.059	-3.375	0.0102 **
Control vs Blue	-0.212	0.809	0.059	-3.571	0.0051 **
Control vs Green	-0.218	0.804	0.058	-3.77	0.0025 **
Control vs Red	0.018	1.018	0.06	0.296	0.9997
Bright white vs Dimmed white	0.198	1.219	0.06	3.295	0.0132 **
Bright white vs Blue	0.183	1.201	0.061	3.01	0.0324 *
Bright white vs Green	0.178	1.195	0.059	2.99	0.0343 *
Bright white vs Red	0.414	1.513	0.061	6.735	<0.0001***
Dimmed white vs Blue	-0.015	0.985	0.059	-0.246	0.9999
Dimmed white vs Green	-0.02	0.98	0.058	-0.353	0.9993
Dimmed white vs Red	0.216	1.241	0.06	3.598	0.0047 **
Blue vs Green	-0.006	0.994	0.059	-0.099	1
Blue vs Red	0.23	1.259	0.061	3.788	0.0023 **
Green vs Red	0.236	1.266	0.059	3.986	0.0011 **

Table 2.2. Summary of the results of post-hoc tests showing the difference between the two locations at the Neck and the Farm. Estimate represent log-transformed differences in bird count between light on and off of experimental and control pairs compared between two locations ***P < 0.001; **P < 0.01; *P < 0.05.

Comparisons	Estimate	Odds Ratio	s.d.	t ratio	p-value
Control: Farm vs Neck	0.0004	1	0.082	0.005	1
Bright white: Farm vs Neck	0.238	1.269	0.087	2.746	0.0679
Dimmed white: Farm vs Neck	0.177	1.194	0.083	2.139	0.2688
Blue: Farm vs Neck	0.154	1.166	0.085	1.819	0.4539
Green: Farm vs Neck	0.107	1.113	0.081	1.32	0.7740
Red: Farm vs Neck	0.15	1.162	0.086	-1.735	0.5091

Table 2.3. Summary of the results of post-hoc tests showing the effect of the brightness of the night on the difference in experimental pairs (‘on’ vs ‘off’) comparing to the control pair (‘off’ vs ‘off’). Estimate represent log-transformed differences in counted birds between light on and off. It shows how red colour caused a (1 – 0.778) *100% = -22.2% decrease in the number of flying birds for every 1 unit increase when the light was turned on during dark nights compared to moonlit nights. ***P < 0.001; **P < 0.01; *P < 0.05.

Comparisons	Estimate	Odds Ratio	s.d.	t ratio	p-value
Control vs Bright	-0.171	0.843	0.094	-1.820	0.0693
Control vs Dimmed	0.045	1.046	0.09	0.496	0.6203
Control vs Blue	-0.112	0.894	0.092	-1.221	0.2224
Control vs Green	-0.105	0.9	0.091	-1.149	0.2508
Control vs Red	-0.251	0.778	0.096	-2.610	0.0093 **

The interval experiment: Our GAM for the interval experiment was well fitted with 95.3% of the deviance explained. The numbers of shearwaters observed increased with the light intensity and the duration of illumination during the 20-minute intervals (for both the dimmed and bright light treatments), as well as the 10-minute bright light treatment (Table 2.4, Fig. 2.5B, Fig. 2.6). There was a 46 % (95% CI [30, 58]) decrease in counted birds when we turned on the bright white light for 20 minutes compared to the control pair (‘off’, ‘off’), a 33 % (95% CI [13, 49]), decrease when we turned on the dimmed light for 20 minutes, and a 27 % (95% CI [7, 42]), decrease when the bright light was turned on for 10 minutes. The smoothed terms of time relative to midnight, as well as the random effects of pair and calendar day showed significant effects on the numbers of the birds counted **(**Table S2.2).

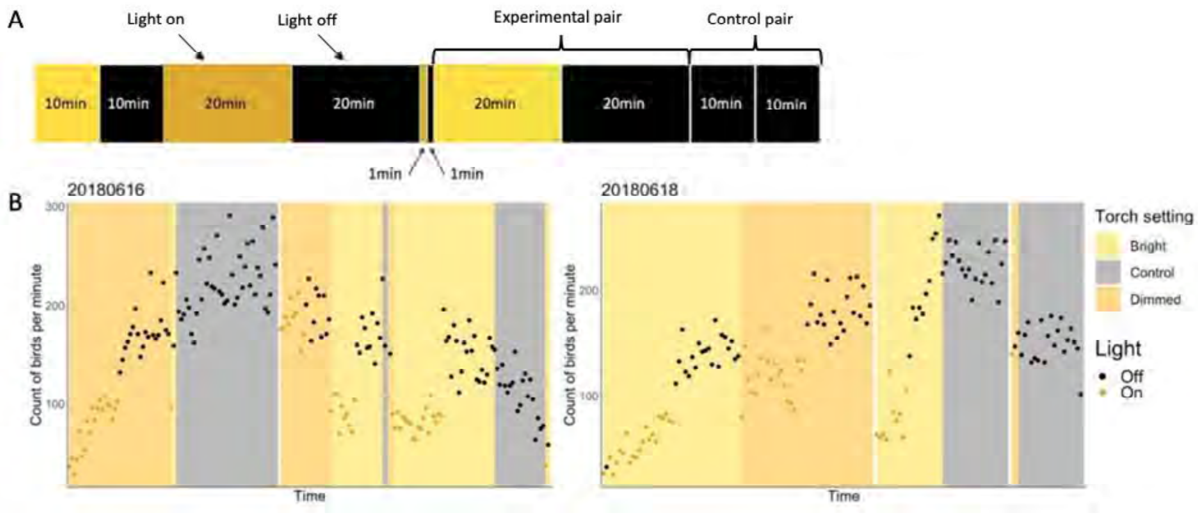

Figure 2.5. (A) Visualisation of treatment series of the interval experiment. Each segment corresponds to the colour (yellow = bright white, orange = dimmed white) and time that the light was on (or off). In the experimental pairs, we turned the light on and off for different lengths of time (1-, 10- and 20-minute intervals). In the control pairs we turned the light off for two consecutive intervals (‘off’, ‘off’) **(B)** Two example days, 16th and 18th June 2018, of the interval experiment starting at 22:43 and 22:50BST respectively. The graphs show the count of birds per minute against the time. Different colour bars represent different torch settings (bright white, dimmed white and control) and two colours of the dots represent light on (yellow) and off (black).

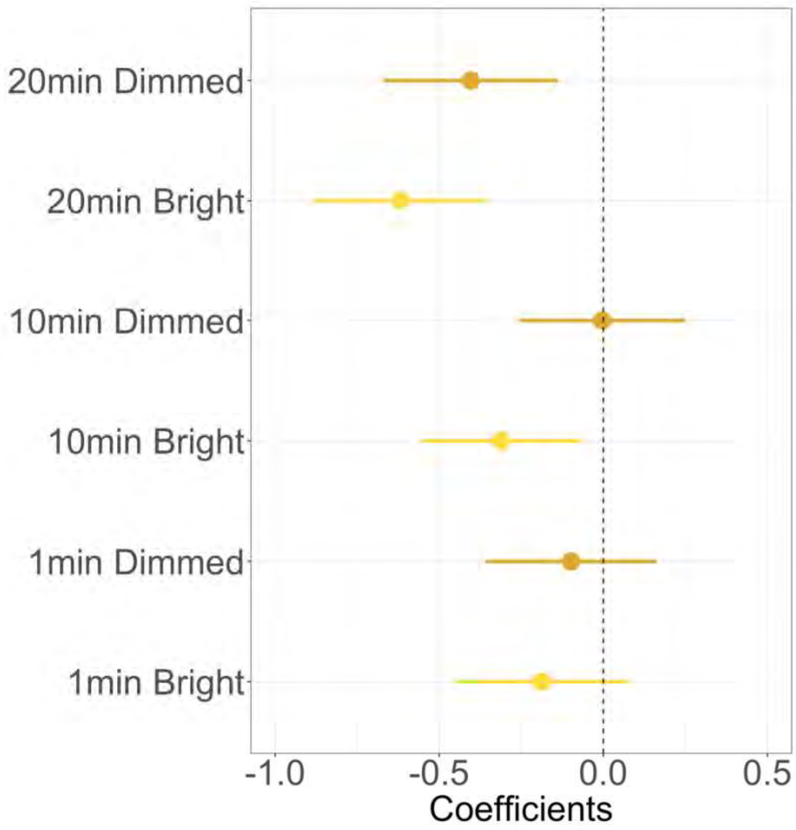

Figure 2.6. The graph represents the results of post-hoc test in the interval experiment. It shows the coefficients of six experimental pairs when comparing the difference in light on vs light off to the control (light off vs light off, dashed line). It showed that both 20-minute treatments, as well as the 10-minute bright treatment, had a significant effect on the number of birds, whereas the 10-minute dimmed treatment and both 1min treatments were not. For detailed statistics, see Table 2.4.

Table 2.4. Summary of the results of post-hoc pairwise tests for interval experiment. Estimates taken from GAM (interval experiment) show log-transformed differences in counted birds. For example, 20-minute bright white caused a (0.539 – 1) * 100% = -46.1% decrease in counted birds when we turned on the light compared to 20-minute control pair (‘off’, ‘off’). ***P < 0.001; **P < 0.01; *P < 0.05.

Comparisons	Estimate	Odds Ratio	s.d.	t ratio	p-value
1min Control vs 1min Bright	-0.187	0.829	0.132	-1.415	0.1605
1min Control vs 1min Dimmed	-0.098	0.906	0.131	-0.750	0.4554
1min Dimmed vs 1min Bright	-0.089	0.915	0.126	-0.710	0.4797
10min Control vs 10min Bright	-0.311	0.733	0.122	-2.540	0.013*
10min Control vs 10min Dimmed	-0.003	0.997	0.127	-0.026	0.9796
10min Dimmed vs 10min Bright	0.308	1.36	0.129	2.378	0.02*
20min Control vs 20min Bright	-0.619	0.539	0.131	-4.712	<0.0001***
20min Control vs 20min Dimmed	-0.404	0.668	0.134	-3.017	0.003**
20min Dimmed vs 20min Bright	-0.215	0.807	0.135	-1.588	0.116

DISCUSSION

Anthropogenic light impacted the nocturnal flight behaviour of Manx shearwaters at a breeding colony, in particular there were effects due to wavelength, brightness and duration of light. We found fewer adult Manx shearwaters in flight when the light was turned on. This was in contrast with our a priori prediction based on the attraction of many bird species including shearwaters to areas of light pollution (Rodríguez *et al.*, 2017; Van Doren *et al.*, 2017; McLaren *et al.*, 2018). However, our finding is not entirely unprecedented. Analysis of radar data revealed the first evidence of birds avoiding bright areas and light of aircrafts during their migration (Larkin *et al.*, 1975; McLaren *et al.*, 2018; Cabrera-Cruz *et al.*, 2020). Another study showed that adult Scopoli's shearwaters (*Calonectris diomedae*) might be perturbed from provisioning their chicks due to an outdoor disco event (Cianchetti-Benedetti *et al.*, 2018), although the study did not separate the effects of disturbance from high-intensity light and sound. Thus, to our knowledge, we provide the first experimental evidence that birds may be repelled by artificial light.

There are two potential explanations for the decrease in the number of birds we observed: grounding and repulsion. Grounding may have reduced the number of flying birds recorded by our thermal camera if adult Manx shearwaters performed the same behaviour as fledglings (Syposz *et al.*, 2018) and landed on nearby land or water, thus decreasing the number of flying birds in the vicinity. Supporting evidence for this hypothesis comes from a study undertaken during foggy weather showing that adult Manx shearwaters are more likely to hit an illuminated structure than a dark one (Guilford et al. 2019).

Furthermore, higher intensities of ALAN are associated with a higher probability of finding grounded birds (Glass and Ryan, 2013; Miles et al., 2010; Reed et al., 1985; Rodríguez et al., 2014), which is consistent with the pattern found in our study. However, while we cannot rule it out, we think grounding is unlikely to explain our results. First, studies of Manx shearwater grounding consistently report only a small number of grounded adults (Rodríguez *et al.*, 2008; Miles *et al.*, 2010; Syposz *et al.*, 2018), in agreement with other reports concluding that the grounding of adults is very rare among Procellariiformes (Le Corre et al., 2002; Rodríguez and Rodríguez, 2009; Telfer et al., 1987). Second, if our experiment had caused enough birds to ground to result in a decrease in the number of flying birds of the magnitude we found, we would have likely observed or heard many of birds crashing on the ground nearby. However, we did not notice any signs of grounding during the whole experiment.

We therefore believe light repulsion (negative phototaxis) is a more likely explanation for our results, in other words that adult Manx shearwaters avoided the light. This would suggest contrasting responses to light from adult and young birds, which could potentially be caused by differences in the developmental stage of the eyes of Procellariiformes. Indeed, it has been suggested that eyes of young burrow-nesting seabirds are not fully developed upon fledging, thus possibly resulting in attraction towards light (Atchoi, Mitkus and Rodríguez, 2020). Avoidance of light may develop later over the birds' lifetime and as their eyes finish their development, but the mechanisms underlying this remain unclear. A more likely explanation is that adult seabirds avoided the light, because it was a new, unknown stimulus near their nest, resulting in neophobia (Cocking *et al.*, 2008; García *et al.*, 2019). Furthermore, our findings indicate that light avoidance in Manx shearwaters is not site-specific, as it occurred at two sites, including one with no human access and one regularly disturbed by human presence at night, which shows that the birds in the latter area were not habituated to nocturnal light stimulus. Further studies investigating the reaction of other adult Procellariiformes to light pollution would be useful to determine whether our unexpected findings apply to other species and to unveil the mechanisms driving negative phototaxis in adult seabirds.

Influence of light spectrum and intensity on shearwaters' nocturnal flight

Another objective of our experiments was to identify whether Manx shearwaters respond differently to red, green, blue, dimmed and bright broadband white colours. Based on previous studies, we expected to find a greater impact of light with increasing intensity and with decreasing wavelength. In accordance with our predictions, we observed greater repulsion when using bright white light than dimmed white light, although as discussed above the effect was measured as a repulsion rather than attraction to the light. In further support of our predictions, we observed that the magnitude of the response was greater when using short compared to long wavelengths, as birds were more repulsed by green/blue than red light. We expected this interaction between brightness and wavelength with any effect (attraction or repulsion) of light since examination of retina of closely related species revealed that seabirds are more sensitive towards blue and green colours than red (Hart, 2004).

We controlled for the intensities of different colours (red, green or blue) using luminosity (an absolute measure of light), rather than specifically for the visual sensitivity of Manx shearwaters. Without a detailed understanding of the visual perception of Manx shearwaters it is hard to conclude whether birds were more influenced by a specific colour of light or if the decrease in the number of birds flying was caused by the higher perceived intensity of the light itself. Since birds were less repulsed by red light, especially on brighter nights, we do consider that darker nights created enough contrast for a bird to perceive the red light and thus induce avoidance behaviour, therefore giving support to the latter explanation. For mitigation purposes, the reason why certain lights have more or less effect is of secondary importance, so our key result here are that dimmed white light and red light caused less disturbance than bright white light and blue/green light respectively. We nonetheless suggest that further research should consider the role of background light on the perception and behaviour of animals towards the light.

Influence of the duration of light pulses on shearwaters' nocturnal flight

Another objective of our experiments was to identify whether longer duration light illumination would cause a stronger response from birds. We found that the longer the light was turned on, the fewer birds appeared in the filmed area. Despite the fact that Manx shearwaters avoided the light, our findings follow the same pattern as described in previous research investigating the influence of the duration of light-on pulses on the attraction of birds towards light (Tufts, 1928; Baldwin, 1965; Avery, Springer and Cassel, 1976; Wiese *et al.*, 2001; Evans *et al.*, 2007; Gehring, Kerlinger and Manville, 2009). We only detected an effect of light on the number of flying Manx shearwaters when using pulses of 20 minutes (for both dimmed and bright light) and 10 minutes (bright light only). In contrast, having the light on for only 1 minute in the interval experiment did not show any effect regardless of intensity. This can initially appear to be at odds with the significant results of our first experiment where 1-minute pulses of white light led to a reduction in the number of flying birds. On further inspection this discrepancy is likely due to the lower statistical power in our interval experiment, which may not have been sufficient to detect a significant difference. Looking qualitatively at the direction of the (non-significant) effect suggests that with a greater sample size we might have observed an effect consistent with the spectra experiment. Therefore, we advise caution when interpreting this result as a negative and recommend that it is repeated in future with greater sample size to disentangle the relative effects.

Conservation implications

Our study shows that the response of Manx shearwater adults to anthropogenic light during nocturnal colony attendance markedly differs from that of fledglings on their first flights. Our experiments demonstrate that adults are repelled by artificial light, in contrast to the apparent attraction of fledglings to light which causes them to ground in coastal towns.

Decreasing light pollution by covering the upward spill of light, choosing correct lighting or reducing the time that the light is on, have been already recommended for areas where Procellariiformes fledglings ground (Reed, Sincock and Hailman, 1985; Rodríguez, Dann and Chiaradia, 2017). Our findings provide evidence for the same mitigations to be considered at or near breeding colonies of burrow-nesting nocturnal seabirds. We show that lights at or near the colony can result in avoidance behaviour from adult Manx shearwaters, and attendance to the burrow might therefore be perturbed (Cianchetti-Benedetti *et al.*, 2018). As a result, we recommend that any unnecessary lights should be avoided. If lights cannot be avoided, using long wavelength light, such as red-filtered light, should be preferred to short or broadband wavelengths. Furthermore, we found tentative evidence that a shorter light-on pulse caused less disturbance in birds and thus, we recommend that the light in structures like lighthouses should be flashing instead of fixed. Short wavelengths, long light-on pulses and stronger light intensity seem to have a stronger effect on behaviour and physiology of a range of species (Baldwin, 1965; Wiese *et al.*, 2001; Lockley, Brainard and Czeisler, 2003; Evans *et al.*, 2007; Gehring, Kerlinger and Manville, 2009; Rodríguez *et al.*, 2017; Wilson *et al.*, 2018; Fischer, Gangloff and Creed, 2019; Timothy, Samiala and Okrikata, 2019; Williams *et al.*, 2019). Thus, these guidelines are likely to be beneficial for many nocturnally active animals, but we also recognise that a taxon-specific approach is necessary when investigating the impact of light pollution on animals.

Finally, our unexpected finding of light avoidance behaviour in Procellariiform seabirds is indicative that we still understand little about how light may impact animals at different stages of life and of the annual cycle. The impact of light avoidance, unlike attraction, might be harder to detect in animals since it may not lead to easily observable and measurable indicators such congregation, grounding or collisions. Light avoidance by

Procellariiformes might be a beneficial reaction in situations where lights might be unavoidable, such as ice lights used as an essential navigation aid in the Southern Ocean (Black, 2005). Nevertheless, light avoidance can still have negative effects by altering and restricting animals' movements, resulting in lower individual fitness and changes to the distribution of populations (Beier, 1995; Nakamura and Yamashita, 1997; Summers, 1997; Kuijper *et al.*, 2008; Cabrera-Cruz *et al.*, 2020). We would therefore like to encourage more research into the impact of light pollution on animals at various locales and during different stages of life, with a special focus on those species which might avoid light.

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SUPPLEMENTARY MATERIAL

Table S2.1 The Cokin® gel filters used during the experiment.

Torch settings	Filter type
Control	None
Bright white	None
Dimmed white	210 + 209 x 2
Blue	721 + 209
Green	139 + 298
Red	160

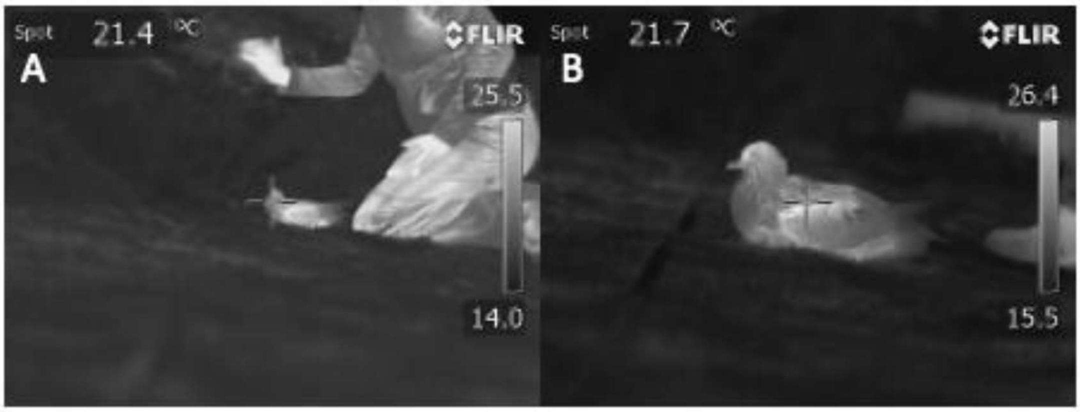

Figure S2.1. Two photos showing a bird 4m (**A**) and 2m (**B**) away from the camera. The Motion-Based Multiple Object Tracking module in MATLAB (R2017a) recognised moving objects bigger than 20 pixels and smaller than 4000 pixels. The approximate calculations revealed that it would mean that birds were minimum 5m away and maximum 85m away from the camera.

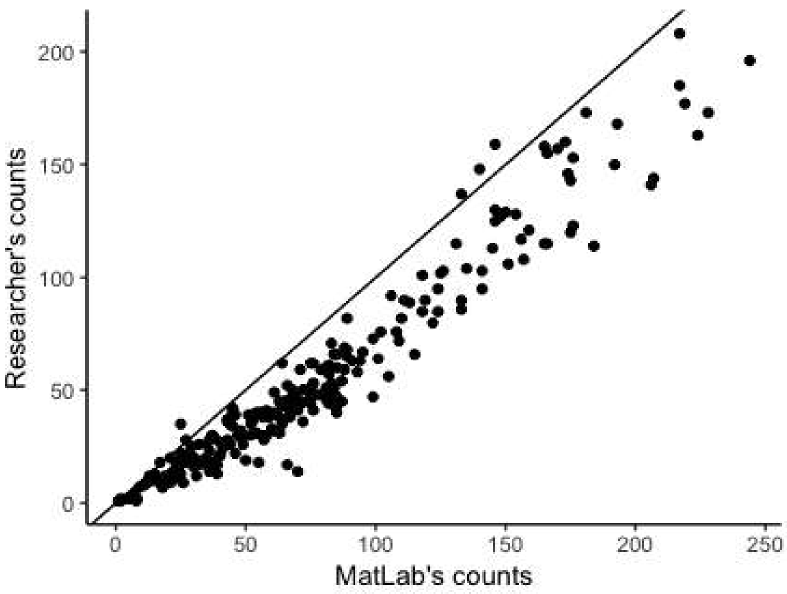

Figure S2.2. The comparison between counts of birds performed by the Motion-Based Multiple Object Tracking module in MatLab and by a researcher (the Pearson Correlation test sample estimates was 96.72% ± 0.93%, t_{238} =58.791, $p < 0.001$).

Table S2.2. Summary of the smooth and random terms of GAMs for the spectra and interval experiments. ***P < 0.001; **P < 0.01; *P < 0.05.

Smooth terms of GAMs for the spectra exp.	edf	Ref.df	Chi.sq	p-value
s(Pair)	365.36	495	2031.8	< 0.0001 ***
s(Calendar day)	7.89	8	11616.68	< 0.0001 ***
s(Time relative to midnight)	5.937	6.22	74.94	< 0.0001 ***
Smooth terms of GAMs for the interval exp.				
s(Pair)	52.272	77	267.12	< 0.0001 ***
s(Calendar day)	8.691	9	4872.08	< 0.0001 ***
s(Time relative to midnight)	5.518	6.354	33.26	< 0.0001 ***

Chapter 3

An assay to investigate factors influencing initial orientation in nocturnally fledging seabirds.

Martyna Syposz, Oliver Padget, Joe Wynn, Natasha Gillies, Annette L. Fayet and Tim Guilford

ABSTRACT

The first solitary migration of juvenile birds is difficult to study because of a low survival rates and sometimes long delays in return to the breeding grounds. Consequently, little is known about this crucial life event of many bird species, in particular the sensory guidance mechanisms facilitating their first migratory journey. Initial orientation during the first migration is a key measure to investigate these mechanisms. This study represents the first application of an assay to measure initial orientation in nocturnally fledging juvenile seabirds. We dorsally deployed a coloured LED on juvenile birds to allow researchers to observe the vanishing bearings of individuals as they flew out to sea for the first time. Additionally, we co-deployed either a small Neodymium magnet or glass bead (control) on top of the bird's head to investigate the use of magnetoreception, previously unexplored in this early life stage.

We used this assay to observe successfully the first flight of fledging Manx shearwaters (*Puffinus puffinus*), which are transequatorial migrants, and found that they did not orient towards their wintering ground during their initial flight. Further, we did not find an effect of the magnetic treatment on juveniles' orientation, though whether this is due to the birds not using magnetoreception, an abundance of other salient cues being available or a simple lack of motivation to orient to the migratory beeline on first flight is unclear. We were, however, able to identify wind direction and topography as drivers of first orientation in Manx shearwaters. Young seabirds fledge with wind component somewhere between a crosswind and a tailwind and their maiden flight is directed towards the sea and away from the land.

This novel assay will facilitate the study of the maiden flight of nocturnally fledging birds and will help advance the study of sensory guidance mechanisms underpinning migratory orientation in a wide range of taxa, including species which are traditionally challenging to study.

INTRODUCTION

Annual migration away from breeding grounds is undertaken by many species in a range of taxa (Brower, 1996; Perryman and Lynn, 2002; Itoh, Tsuji and Nitta, 2003; Guilford *et al.*, 2009; Egevang *et al.*, 2010). This movement towards more productive areas is a crucial behaviour to ensure fitness and survival (Newton, 2008; Harrison *et al.*, 2011). While in some species juveniles simply follow adult conspecifics on their first journeys (Valenzuela *et al.*, 2009; Harrison *et al.*, 2010; Mueller *et al.*, 2013), the mechanisms underpinning the first migration of juvenile animals which migrate separately to adults remains puzzling (Bingman and Cheng, 2005). All of the information for the first lone migration must be inherited or learnt prior to fledging (Liedvogel, Åkesson and Bensch, 2011). Studies investigating the behaviour of wild birds have revealed evidence for inheritance of migratory direction in small passerines (Perdeck, 1958; Berthold *et al.*, 1992; Helbig, 1994; Berthold, 1999). Some evidence has been also found in seabirds. During their first migration, young streaked shearwaters (*Calonectris leucomelas*) were observed to fly hundreds of kilometres over the landmass of Japan, possibly following their inherited migratory vector (Yoda, Yamamoto, *et al.*, 2017). It is unclear, however, whether inherited migratory vector is the norm for other species. The low survival rate (as compared to adults), high dispersal and, sometimes, years spent far from breeding grounds before recruitment make collecting information about this life stage, even with modern dataloggers, extremely difficult (Shillinger *et al.*, 2012). Consequently, for many species of bird, the destination of first-time migration for juveniles remains unknown and the learning and sensory guidance mechanisms that have evolved to facilitate such unguided autonomous movement still remain unknown.

Recent improvements in the accuracy, data quality and miniaturisation of biologging technology have permitted the collection of much more detailed information about the flight behaviour of birds (e.g. Lord et al. 1962, Wikelski et al. 2007, Robinson et al. 2010, Guilford et al. 2011). For example, tracking studies in juvenile raptors (Sergio *et al.*, 2014; Harel, Horvitz and Nathan, 2016) and seabirds (Riotte-Lambert and Weimerskirch, 2013; de Grissac *et al.*, 2016, 2017; Collet *et al.*, 2020) reveal that young birds tend to be more affected by wind conditions in their initial flights than adults, suggesting a mechanism of learning and improvement of flight mechanics (Fayet, 2020). There is, however, an inevitable trade-off when tracking all but the largest birds between the weight, size and cost of devices, the quality and amount of the resulting data (Wilson *et al.*, 2004; Shillinger *et al.*, 2012; Venabeele *et al.*, 2015; Bodey *et al.*, 2018). Furthermore, while transmitting devices might in future allow more flexible tracking of animals without the need to be recovered, currently the majority of affordable devices must be retrieved from the animal to download the data, and consequently cannot be used on individuals which are unlikely to be captured again. This is particularly the case for fledgling birds with high degrees of dispersal, low survival, or a long breeding deferral period.

Another means to collect relevant orientation data from animals without the need for tracking technology is to infer aspects of animals' orientation behaviour through behavioural assays. One such example is the Emlen funnel (Emlen, 1975) which comprises a paper funnel with an ink well at the centre. Placing songbirds in the funnel overnight results in ink staining indicative of the direction that the bird was trying to escape the tunnel in. Many modern, automatic modifications (Bianco *et al.*, 2016) have now been used to identify initial orientation in a range of night-migrating passerine species by recording the directional activity of birds in a cage with a circular bottom. These methods can be used to achieve a large sample size at a relatively low cost but are not suitable for larger avian species. Prior to the development of GPS tracking devices, which have now been used extensively in navigation studies of homing pigeons *Columba livia* (Biro *et al.*, 2002; Gagliardo *et al.*, 2009; Armstrong *et al.*, 2013), an assay was developed to identify the vanishing bearings, a proxy for initial orientation, of larger birds (at the time, mainly pigeons, Kramer and von Saint Paul, 1950a, 1950b; Matthews, 1951; Kramer, 1953). Under this method, observers use binoculars to manually track a bird's flight trajectory following its release. Once the bird disappears from the observers' view, its orientation is recorded. Sandberg et al. (2000) modified this assay to observe nocturnally migrating passerines by dorsally attaching lightsticks and observing the light via binoculars. The initial orientation of red-eyed vireo (*Vireo olivaceus*) and northern waterthrush (*Seiurus noveboracensis*) measured using such vanishing bearings was correlated with the bearing from orientation cages (Sandberg *et al.*, 2000). This method, however, was developed for small adult passerines and has not been applied to any other species of bird.

These assays have helped to determine the navigational mechanisms which facilitate the migration of birds. In particular, they have helped shed light on the role of magnetoreception in providing a compass bearing during migration for some species (e.g. Wiltschko and Gwinner 1974, Sandberg et al. 2000, Muheim et al. 2002, Wiltschko and Wiltschko 2006), but how widespread the magnetic compass is across taxa remains unknown. Whilst night-migrating songbirds are hypothesised to make use of a light-mediated magnetic inclination compass (ostensibly located in the retina of the eye, Hein et al. 2010) in combination with celestial cues to control orientation during migration (Muheim, Bäckman and Åkesson, 2002; Wiltschko and Wiltschko, 2002), evidence for a role of a magnetic compass is much more equivocal across other avian taxa. In seabirds, for example, numerous attempts to disrupt any putative magnetoreceptor—using a jostling rare earth magnet inside a box attached to the bird's head—found no evidence for a role of a magnetoreception during large-scale movements (Massa *et al.*, 1991; Benhamou *et al.*, 2003; Benhamou, Bonadonna and Jouventin, 2003; Bonadonna *et al.*, 2003, 2005; Mouritsen, 2003; Pollonara *et al.*, 2015; Padget *et al.*, 2017). These studies however were all conducted in adult birds, and so a magnetic compass remains a potential candidate at least for movement on first migration (Liedvogel, Åkesson and Bensch, 2011).

Here, we aimed to (i) adapt an assay (Sandberg et al. 2000) for the study of initial orientation in large numbers of nocturnal fledging young seabirds, and (ii) use this to test which environmental variables fledglings are attending to when embarking on their maiden flight. Specifically, we were interested in whether access to the undisturbed geomagnetic field is crucial to initial orientation in a nocturnal migratory seabird, the Manx shearwater (*Puffinus puffinus*), during fledging. In many species of bird, young, inexperienced individuals are known to be particularly affected by environmental variables during fledging, especially wind (Riotte-Lambert and Weimerskirch 2013; de Grissac et al. 2016; de Grissac et al. 2017; Collet et al. 2020). Thus, we additionally investigated the role of wind and topography in determining the initial orientation of Manx shearwater fledglings on their first flight.

METHODS

Species and site

Manx shearwaters (*Puffinus puffinus)* are burrow-nesting seabirds from the order Procellariiformes. They are mainly active during the day and rest during the night (Shoji *et al.*, 2016). However, during the breeding season, they visit their nests exclusively at night, possibly to avoid predation (Watanuki, 1986; Keitt, Tershy and Croll, 2004; Silva *et al.*, 2011). Similarly, young, burrow nesting Procellariiformes leave their nests only during the nights to exercise their wings and build their flight muscles (Yoda, Shiozaki, *et al.*, 2017). Manx shearwater chicks begin life entirely covered in insulating down feathers that are progressively lost through their later development, with most birds losing the majority of their down prior to fledging (Warham, 1990; Leonard and McKee, 2005). Ringing and biologging data suggest that young Manx shearwaters spend first winter in the South Atlantic in waters along the Patagonian shelf (Fig. 3.1A**,** Brooke 1990, Guilford et al. 2009).

The study was undertaken on Skomer Island, Wales (51˚ 44' N, 5˚ 17' W, Fig. 3.1B), the biggest colony of Manx shearwaters in the world, with around 317,000 breeding pairs (Perrins *et al.*, 2012). The island is located in St. Brides Bay within a kilometre of the

Pembrokeshire coast (Fig. 3.1C). To reduce geographical biases, two locations on Skomer Island were chosen for this study, Skomer Head and Pigstone Bay. Both locations are near to a high concentration of Manx shearwater burrows and are coastal and west-facing, with a view of the sea along a large arc of the horizon. Locations where coastal developments and ships could be seen prominently were avoided owing to the known effect of light pollution on shearwaters soon after fledging (e.g. Syposz et al. 2018). The area around Skomer Island, however, is surrounded by light pollution from the coast of Wales, and thus it was inevitable that part of the horizon was lit. The attraction of fledging shearwaters to light is known to be lower on moonlit nights (Miles *et al.*, 2010; Syposz *et al.*, 2018), so we collected additional data on fledgling orientation on both moonlit and moonless nights (Fig. S3.2). The local geomagnetic characteristics of Skomer Island during the study were as follows: intensity = 48789nT (Secular Variation = 31), inclination = + 66.488° (SV = - 0.3), declination = - 2.15° (SV = 11.7, IGRF, 2020).

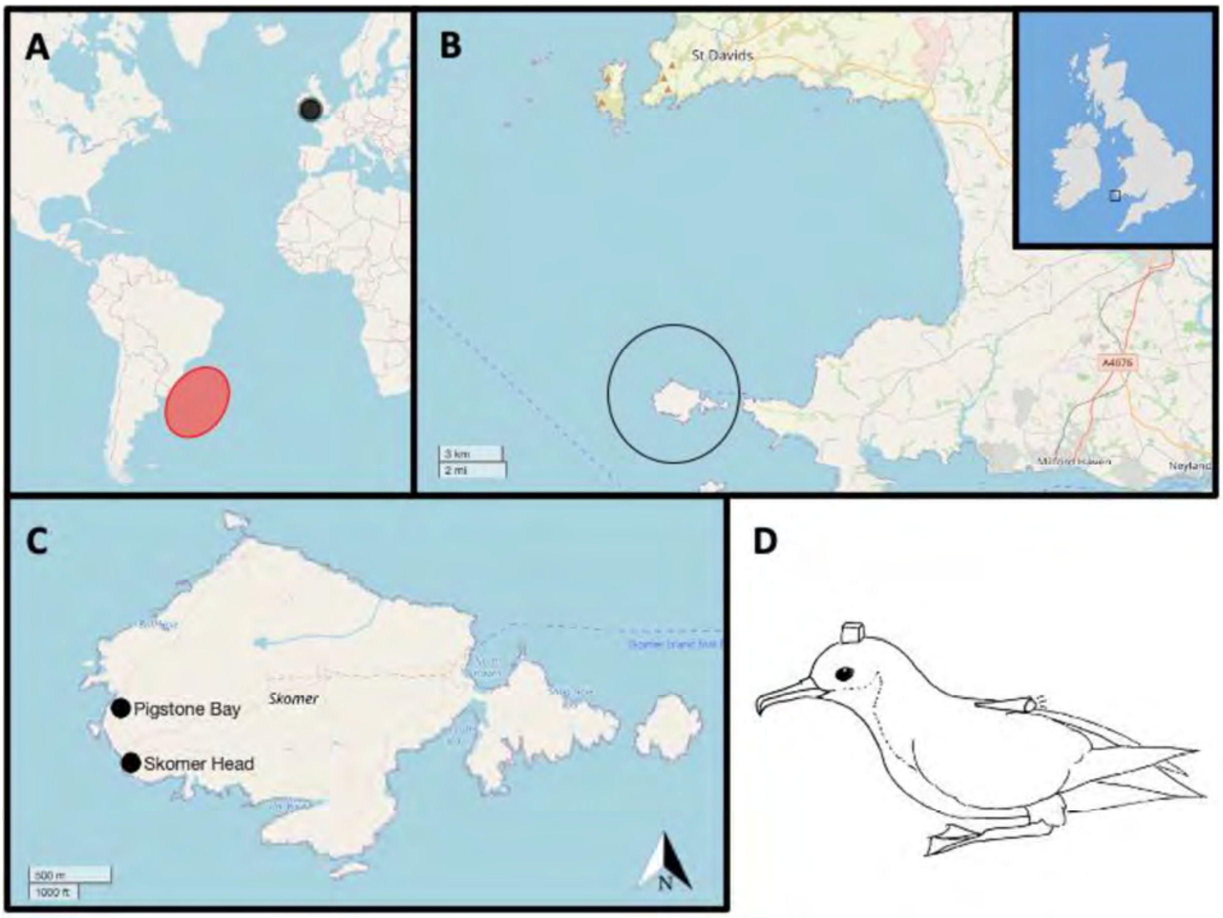

Figure 3.1. (**A**) A map with location of Skomer Island (black dot) and the wintering grounds (red dot) of Manx shearwaters (OpenStreetMap®, 2020a). (**B**) A map of location of Skomer Island (black circle) in St. Brides Bay (OpenStreetMap®, 2020b). (**C**) A map of Skomer Island. Two black dots mark sites, Skomer Head and Pigstone Bay, where the experiment was undertaken (OpenStreetMap®, 2020c). (**D**) A schematic drawing of a Manx shearwater with a box on its head and LED light on its back.

Experimental design

The study was undertaken during the peak fledging period in September 2017 and 2018. Additional data were gathered in 2019 specifically with the aim of assessing the role of moonlight levels on vanishing bearing of seabirds, and these are provided in the supplementary material. Fledgling Manx shearwaters were captured after emergence from their burrows within 500 m of the two chosen release sites. All birds were weighed and were selected to have a low down score (0-1 corresponding to little or no down - the down score is 0 when there is no down visible and 3 if the whole bird has down on all of its body, Perrins 2014). To record vanishing bearings at night, we deployed a small coloured LED on the back of each bird (c. 4g, Fig. 3.1D, Fig. S3.1 Sandberg et al. 2000, Lorne and Salmon 2007). The LED was attached with a thin strip of TESA marine tape laid underneath very small bunches of contour feathers loosely enough that the light would fall off soon after fledgling (this attachment method is a modification of a commonly used protocol for GPS attachments on this species; Guilford et al. 2008). The LED was additionally wrapped in TESA tape to avoid the spill of light towards the bird's head and which could potentially disturb its flight. To test the role of the magnetic field on initial orientation, we fitted a 1cm x 1cm cardboard box on top of each bird's head using a drop of glue applied to the feathers. Each box contained either a strong cylindrical Neodymium magnet (5mm in diameter x 8.47mm thick, mass 1.2g, vertical pull 0.91kg; magnetic treatment) or a glass bead of similar dimensions (control treatment). The magnet was free to tumble inside the box to produce a rapidly varying artificial magnetic field stronger than ambient, hence disrupting the birds' ability to read the earth's magnetic field (as in Pollonara *et al.*, 2015). Each treatment group was assigned a different LED colour each night (green, blue, white and red in 2017 and green and blue in 2018) and observers were blind to the treatments. The study was conducted after ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/6128) and Natural Resources Wales, Skomer Island Advisory Committee.

After fitting the light and magnet, birds were placed on the ground and left to fledge of their own accord. Once a bird took off, a standing observer followed it with binoculars (Nikon Prostaff 8x30) until it vanished from sight. Another observer with a compass, recorded the bearing of the bird using a red head torch to illuminate a notebook. The compass was placed directly below the binoculars and the first observer made sure that it was rotated the body in direction of the flying bird. In 2017 only the vanishing bearing (to the nearest 1º) was recorded and in 2018, bearings were taken every 10 seconds. Birds sometimes disappeared from the observer's view which led to a gap between recordings, in which case the time was noted.

Environmental factors

Meteorological data, including cloud cover, wind direction and wind speed, were collected at least every 32 minutes. An observer measured the cloud cover on a nine-point scale (0 oktas being clear sky and 8 being completely opaque). Wind direction and speed were measured by a handheld Vaavud anemometer (Vaavud ApS, Copenhagen S, Denmark). For safety of observers, releases were not carried out on nights with strong wind (maximum wind speed 16 m/s, mean = 6 m/s, median = 8 m/s). Releases were also not carried out during rainy weather due to the sensitivity of the deployed equipment to water damage. Additionally, we calculated moon illuminance to test for a potential effect of light pollution on fledgling orientation (see Methods in supplementary material for details).

Data analysis

We investigated how the magnetic treatment, wind, and location influenced Manx shearwater fledging direction. Analyses were conducted in `R` (version 1.1.456, R Core Team 2018) using the package ‘`circular`’ (Lund *et al.*, 2017).

First, we conducted a permutation test to determine whether there was a difference in the circular variance (measured as a Rayleigh value) in final vanishing bearings between the magnetic and control treatments, since we expect that disrupted orientation (from the magnetic treatment) would result in initial orientations closer to a random distribution. To account for changes in the environmental variables between days, only days with at least 3 releases per treatment were kept. We calculated each day’s deflection by comparing Rayleigh statistics of all magnetic and control bearings and then calculating the global mean across dates. We then randomised the treatment identity of each bird 1000 times and calculated the global difference between the Rayleigh statistics of magnetic and control treatments for each run. Finally, we used a Rayleigh test, using only the final vanishing bearings of control birds, to examine if unmanipulated Manx shearwaters are oriented towards the wintering grounds during their maiden flight.

For the analysis of the effect of wind direction and topography on the orientation, we used the vanishing bearing from all the days that the experiment was undertaken. We generated a null distribution by randomising the vanishing bearings with respect to wind direction 1,000,000 times and calculated the global mean for each run. We then calculated the actual mean of the angles (0-180º) between the vanishing bearings and wind direction and compared it to the null distribution.

To investigate the influence of topography on seabirds, we divided data into two locations and, further, by four main wind directions (northerly, westerly, southerly, easterly). We tested if birds in each group were significantly oriented using a Rayleigh test. We also conducted Watson-wheeler tests to examine whether there was a difference in orientation between the two locations, controlling for the effect of the wind direction.

RESULTS

Observation performance

We successfully collected data on the orientation of fledging of 95 juvenile seabirds (19 in 2017, 76 in 2018). LEDs were deployed on 169 birds (36 in 2017 and 133 in 2018). Some of the birds did not take off and their devices were subsequently removed (7 – 2017, 35 -2018), while others wandered away, were lost or we failed to collect the data (10 – 2017; 22 – 2018). For analysis, we used data from 93 birds out of 95 observed birds, because two birds landed on the water, so their fledging was marked as unsuccessful. The average weight of a bird used in the study was 416g (median = 420g, SD = 27g, Table 3.1). Observation durations varied from 30sec to 405sec (median = 133sec, SD = 80sec).

Table 3.1. Summary of the schedule of the experiment with dates, average wind direction, wind speed (m/s), number of birds fledged split into control and magnetic treatment, and average weight of birds (grams).

YEAR	DATE	LOCATION	WIND DIRECTION	AVG WIND SPEED (M/S)	NO. OF FLEDGED BIRDS		WEIGHT (AVG IN g)
					Control	Magnetic	
2017	18/09/2017	Skomer Head	WNW	-	7	3	408
	19/09/2017	Skomer Head	SE	-	4	5	396
2018	09/09/2018	Pigstone Bay	W	9.05	2	0	450
	12/09/2018	Pigstone Bay	W	5.83	2	2	442
	13/09/2018	Pigstone Bay	WSW	7.37	2	1	438
	14/09/2018	Pigstone Bay	SW	6.76	4	5	413
	15/09/2018	Pigstone Bay	S	7.92	3	3	408
	16/09/2018	Pigstone Bay	WSW	3.00	2	4	423
	18/09/2018	Skomer Head	SSW	7.85	3	4	421
	21/09/2018	Skomer Head	WNW	7.31	2	3	405
	22/09/2018	Skomer Head	NE	5.10	5	7	404
	23/09/2018	Pigstone Bay	NNW	4.84	5	6	408
	24/09/2018	Pigstone Bay	E	1.87	5	4	404
TOTAL					**46**	**47**	

Influence of magnetic treatment on Manx shearwater bearing

There were 7 days on which the sample size in each treatment was 3 or more, giving an overall sample size of 73 (36 magnetic and 37 control) for this test. A permutation test showed that there was no significant difference in variance between the magnetic and control treatments (permutation test, iteration = 1000, p value = 0.272, Fig. 3.2), indicating that variance in orientation of birds treated with magnets was similar to that of control birds. Furthermore, we investigated if control birds are appropriately oriented towards their wintering ground (SW). A Rayleigh test revealed that control birds were not significantly oriented in any direction (Raleigh test, t = 0.26, p value = 0.088, mean orientation = 263°, Fig. 3.2A).

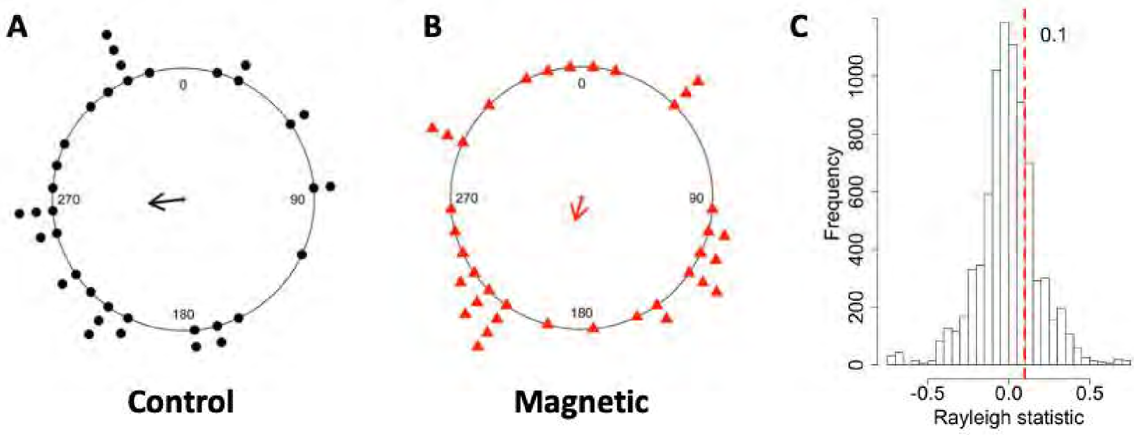

Figure 3.2. (**A**) Control Manx shearwaters orient randomly ($\alpha = 263^{\circ}$, $r = 0.26$, $p = 0.088$). Each black dot indicates the orientation of an individual bird. The arrow indicates the mean orientation of the group ($\alpha = 263^{\circ}$) and its vector length ($r = 0.26$). (**B**) Orientations of experimental birds. Each red triangle indicates the orientation of an individual bird. The arrow indicates the mean orientation of the group ($\alpha = 195^{\circ}$) and its vector length ($r = 0.17$). (**C**) We used a permutation test to examine if the variation in orientation of magnetic and control birds differs. First, we calculated observed global mean of all differences for each day, between Rayleigh statistics of magnetic and control bearings (mean = 0.1, red dashed line). Then, to compute a null expectation (the histogram shown), we calculated global means of all differences for each day between Rayleigh statistics of bearing of 1000 times randomised magnetic and control identities. The calculated p value = 0.272.

Influence of other variables on orientation

To test the effect of wind direction and topography on fledging orientation, we collected all vanishing bearings, because we found no evidence for a difference between control and magnetic birds. The permutation test revealed that birds are more likely to fly in a consistent direction relative to the wind than expected by a chance (iterations = 1000000, n = 93, p value < 0.001, Fig. 3.3A). The average angle between orientation of birds and wind direction was 116° (SD = 44°, Fig. 3.3B, Fig. 3.4).

When taking into account the wind direction and the location of the release site, we found a significant difference between flight orientations in westerly (Watson-Wheeler test, W = 26.812, df = 2, p-value < 0.001) and southerly winds (W = 13.252, df = 2, p-value = 0.0013), whereas in northerly winds, we found no significant difference (Watson-Wheeler test, W = 2.2283, df = 2, p-value = 0.3282; Fig. 3.5). The results suggest that, when taking wind direction into account, the orientation of Manx shearwaters depends on the location of fledging. Each group of birds was significantly oriented (Table 3.2). These orientations, when looking at the topography of Skomer Island, resulted in birds flying away from the land and towards the sea. We found no effect of moonlight levels on orientation (Figure S3.2, supplementary material).

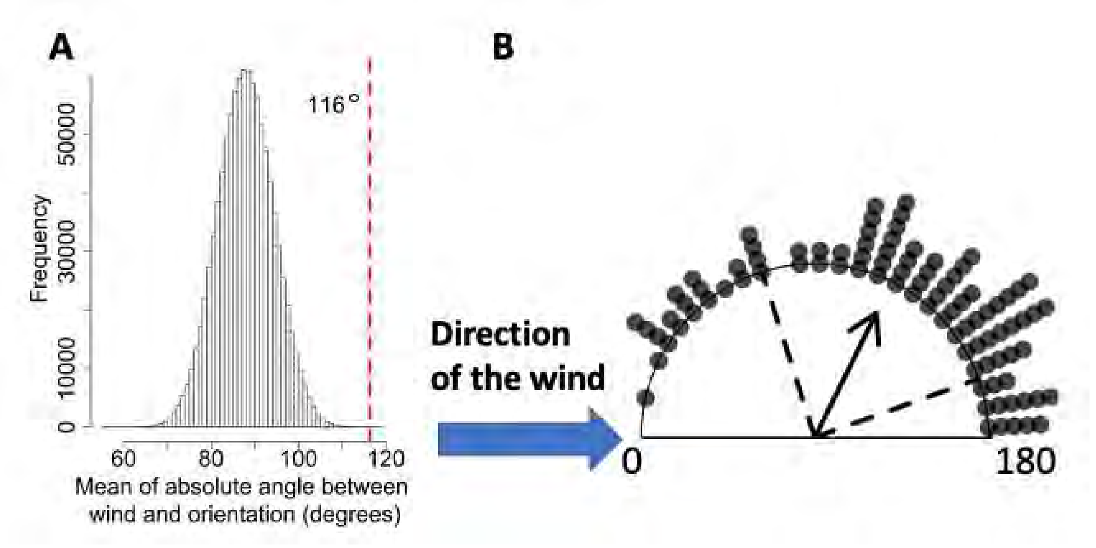

Figure 3.3. (**A**) To examine if wind direction influenced the orientation of young Manx shearwaters, we conducted a permutation test. We generated a null distribution (the histogram shown) by randomising the vanishing bearings with respect to wind direction 1,000,000 times. Then, we calculated the angle (0-180º) between the two directions and the global mean for each run. Next, we computed the observed mean of the angles between the bearing of birds and wind direction (116º, red, dashed line) where the resulting difference in angles was >1%. (**B**) Orientation (0-180º) with respect to wind direction (blue arrow). Each dot represents the angle between an individual bird's vanishing bearing and wind. The arrow indicates mean direction (116º) and the dashed lines represents standard deviation (±44º).

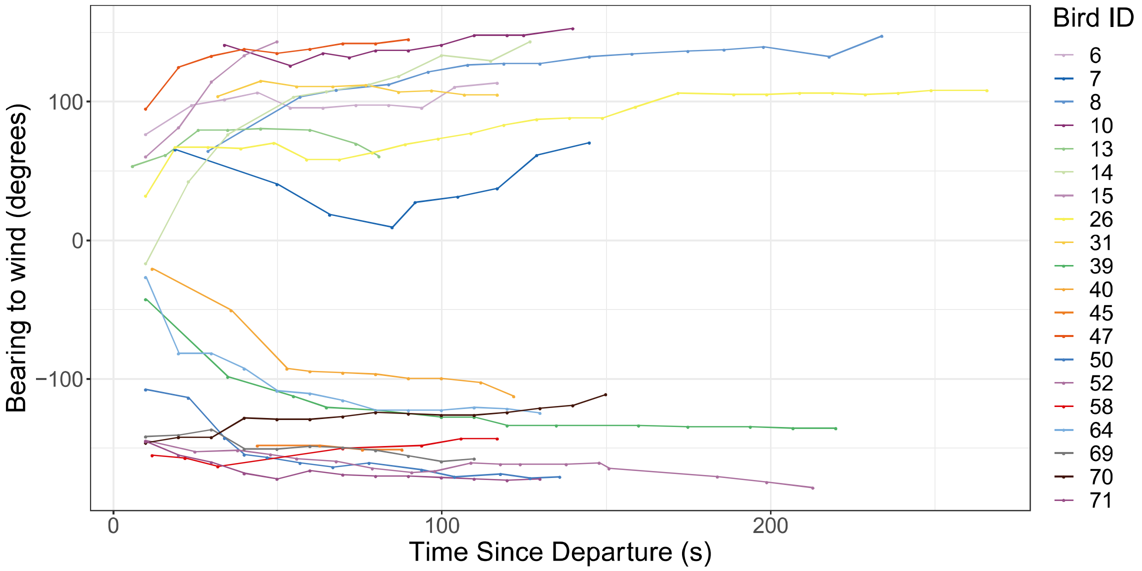

Figure 3.4. A graph representing the change over time (s) of the angle between wind and bearing from observer (from -180º to + 180º). Positive values indicate clockwise angle from the wind direction and negative values – anticlockwise. The coloured lines connect the observations (dots) of each of 20 birds through time up to vanishing. For clarity of the figure, the subset of birds was chosen from 2018 when we recorded bearings continuously during bird's maiden flight.

Table 3.2. Manx shearwater orientation is significant when taking into account the fledging location and wind direction. Table showing the group's sample size, circular mean orientation and the results of Rayleigh tests (Rayleigh value and p value). ***P < 0.001; **P < 0.01; *P < 0.05.

LOCATION	WIND DIRECTION	SAMPLE SIZE	GROUP'S MEAN ORIENTATION (DEGREES)	RAYLEIGH STATISTIC (0-1)	P VALUE
PIGSTONE BAY					
	Northerly	11	230	0.926	<0.001 ***
	Westerly	20	13	0.77	<0.001***
	Southerly	10	334	0.845	<0.001***
	Easterly	9	293	0.884	<0.001***
SKOMER HEAD					
	Northerly	12	219	0.722	0.001**
	Westerly	15	177	0.765	<0.001***
	Southerly	16	104	0.532	0.009**

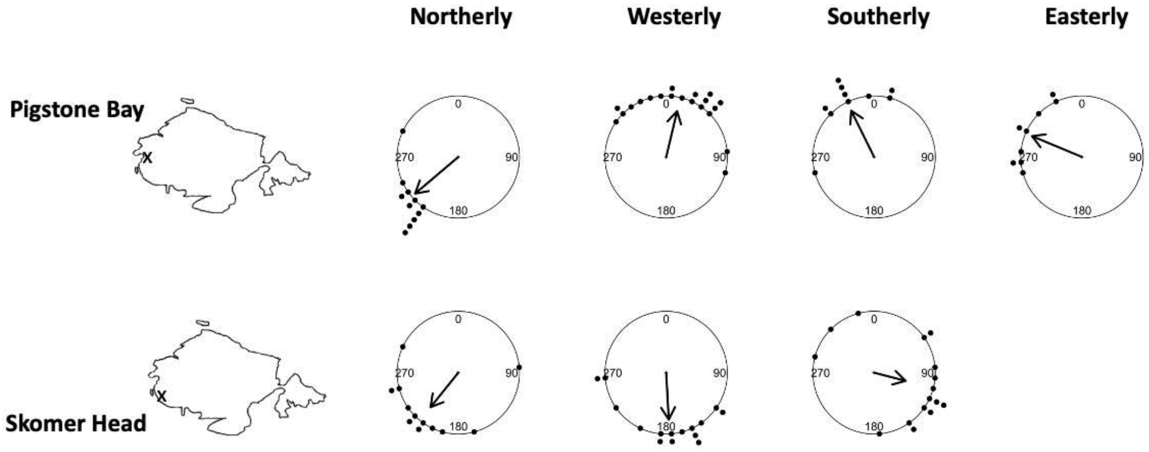

Figure 3.5. The vanishing bearing of Manx shearwaters differed between locations in westerly and southerly, bur not northerly winds. Each circular graph represents a group of Manx shearwaters in one of the four winds (northerly, westerly, southerly and easterly) and one of the two locations (top – Pigstone Bay, bottom – Skomer Head). Each dot represents the vanishing bearing of an individual bird. The arrow indicates each group's mean direction and vector length. Two outlines of a map represent Skomer Island, and the black crosses indicate the location of respective experimental sites on the island (Pigstone Bay & Skomer Head). All graphs are presented in relation to geographic north.

DISCUSSION

In this study we applied an assay to measure the orientation of juvenile migratory shearwaters during their first flight and investigated whether they may use the magnetic field to determine their orientation. Using this minimally-invasive assay, we successfully observed a large number of Manx shearwater fledglings (95 birds) departing from their natal colony at night and investigated the drivers of their initial orientation. The attachment of LED lights to the backs of birds allowed us to observe them for a long time after their take off (up to 6min 45sec) and record their precise bearings. Pairing this with a small, light cardboard box with a rare earth magnet enabled us further to test the magnetic sense of the birds. This cheap and light method could be widely applicable for even smaller species from a range of taxa and thus added to the growing toolkit for tracking birds, which is mostly comprised of expensive devices which are limited to large species. Our assay could be especially useful for fledgling birds, which are unlikely to be captured again, and could expand our understanding of early migratory navigation

Our assay revealed that juvenile shearwaters do not orient towards their wintering ground during the very start of initial flight. Whilst our result is consistent with previous experiments in that we found no difference between magnetically treated and control groups (Massa *et al.*, 1991; Benhamou *et al.*, 2003; Benhamou, Bonadonna and Jouventin, 2003; Bonadonna *et al.*, 2003, 2005; Mouritsen, 2003; Pollonara *et al.*, 2015; Padget *et al.*, 2017), we noted no overall orientation in the control group and as such it is unclear whether juvenile shearwaters do or do not utilise magnetic cues. We cannot determine whether Manx shearwaters utilised other cues available, lacked the motivation to orient to the migratory beeline on first flight or the signal was overridden by environmental variables.

Our assay, however, was successful in identifying wind direction and topography as important drivers of initial orientation of these juvenile seabirds on their maiden flight. All the birds in our study flew with a wind component somewhere between a crosswind and a tailwind when flying away from land. Their orientation was affected by the location from which they began their flight. We found a difference between initial orientation in release locations with southerly and westerly winds. There was no difference, however, in orientation in northerly winds. The topography of land in both release locations allowed only for one crosswind direction (westerly) which would result in birds flying away from land and towards the sea. We suggest that these results further support the conclusion that initial orientation in juveniles is driven by a combination between topography and wind.

Our results revealed that birds tended to fly with a bearing to the wind somewhere between a crosswind and a tailwind, with an average bearing to the wind of 116 degrees. It has been suggested that some juvenile seabirds might be constrained to fly with tailwinds. Collet et al. (2020) and Riotte-Lambert and Weimerskirch (2013) found that young seabirds depart mostly with tailwind directions in their first weeks of exploring, and only after a few weeks do the wind conditions progressively lose influence on their foraging directions, suggesting that juvenile birds require a learning phase of flight and/or navigational skills to overcome wind constraints on flight direction (Riotte-Lambert and Weimerskirch, 2013; de Grissac *et al.*, 2016, 2017; Harel, Horvitz and Nathan, 2016). Wind has been shown to affect flight stability and energetics (Yamamoto *et al.*, 2017) as well as efficiency (Harel, Horvitz and Nathan, 2016) in juvenile birds. Muscle reinforcement and optimal flight practice has to be developed over the first weeks of their life (de Grissac *et al.*, 2017). Thus, fledgling Manx shearwaters from our study might have been buffeted by winds on their maiden flight due to their lack of flight experience. This hypothesis is supported by reports on grounding events in Procellariiformes juveniles in areas with high levels of light pollution, which show an increased number of collected seabirds when the wind was blowing onshore, from the colony towards the light polluted area (Rodríguez *et al.*, 2014; Syposz *et al.*, 2018). It has been proposed that this may be a result of the interaction between wind direction and the effect of light pollution, with inexperienced juveniles blown in the direction of the lights and therefore increasing their chance of being affected by them.

Light pollution alone may also affect the orientation of seabird fledglings on their first flight. Juvenile Procellariiformes are indeed vulnerable to the effects of light pollution (Rodríguez *et al.*, 2017), and so their orientation may be biased towards light-polluted areas (Rodríguez, Rodríguez and Negro, 2015). Testing this hypothesis was beyond the scope of this study and would have required an experimental set up where we could manipulate the level of light pollution, which was not possible at our study colony. However there have been reports of decrease in fallout during the full moon (Telfer *et al.*, 1987; Rodríguez and Rodríguez, 2009; Miles *et al.*, 2010; Syposz *et al.*, 2018) perhaps due to a lower contrast between light polluted and dark parts of the horizon (Miles *et al.*, 2010). We conducted a simple comparison of the orientation of fledglings on a moonlit and a moonless night (supplementary material), but found no difference. This suggest that light pollution may not have affected the orientation of Manx shearwater fledglings in our study, but further orientation experiments, including in more light polluted areas, would be required to confirm this.

CONCLUSION

Here, we developed an assay which facilitated the measurement of initial orientation in juvenile migratory seabirds. We did not find any evidence that Manx shearwaters orient towards the wintering grounds and thus, we were unable to derive any conclusions about the effect of the magnetic treatment on juveniles' orientation. We conclude, however, that wind direction and topography seem to play an important role in orientation at the start of their maiden flight. This minimally-invasive, simple and cheap assay facilitates the study of the first flight of a large number of nocturnally migrating birds and could be used in a range of taxa. This could help to understand questions that require large sample sizes and investigate the sensory guidance mechanisms underpinning the flights of species which are typically difficult to research, due their difficulty in recovery, or their unsuitability for large biologging devices.

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SUPPLEMENTARY MATERIAL

Figure S3.1. LEDs used for the experiment in their casing (top left) and after the casing were taken off (top right). Bottom picture shows a box of ready for experiment LED lights, batteries and LEDs ready to be assembled. There are two lights in the middle: one in a full hoodie made of tesa tape (blue), and one without a hoodie (green).

Investigating the effect of moonlight on the flight of fledging Manx shearwaters

Methods

The collection of the data in 2018 resulted in covariance between wind direction and moon phase, thus we additionally undertook the experiment in 2019. We deployed devices on 19 birds on two nights (15th & 22nd September) and collected vanishing bearings from 14 of them. Four of the birds did not take off and their devices were removed, and one bird was lost. In this year, birds had only LEDs attached as we were not interested in influence of magnetic treatment on their vanishing bearing, but on disentangling the effects of moonlight and wind.

For the analysis, we collated the data from all three years of the study (2017, 2018, 2019). To calculate the moon illuminance on each night, we used a method that presents moon intensity as perceived on the earth when taking into account some astronomical variables (Austin, Phillips and Webb, 1976; Rubolini *et al.*, 2015). Additionally, we weighted the moon illuminance by rescaled cloud cover factor (1 – clear sky and 0.5 – full cloud cover). The moon presence (Yes/No) was defined as present if the arbitrary moon intensity was above 3.23. We calculated this threshold using moon illumination using the `R` package ‘`segmented`’ (Muggeo, 2017) and data from Chapter 5. Moon illumination is known to influence grounding in Manx shearwaters, with higher fallout predicted when moon illumination is between 0-3.23 (little/no moon) and a lower number of predicted groundings above the 3.23 threshold (Chapter 5). We conducted a permutation test to determine the effect of moonlight on departure orientation. We calculated the observed difference between the circular mean of birds released with moon presence and without. We then randomised the treatment identity (moon or no moon) of each bird 1000 times and calculated the global difference between the circular mean of birds released with moon present and without moon influence.

Results

The permutation test showed that there was no difference in mean orientation between days with and without moon presence in Pigstone Bay (southerly: n = 15, p = 0.245; westerly: n = 29, p = 0.177) and at Skomer Head (westerly: n = 15, p = 0.531, Fig. S3.2).

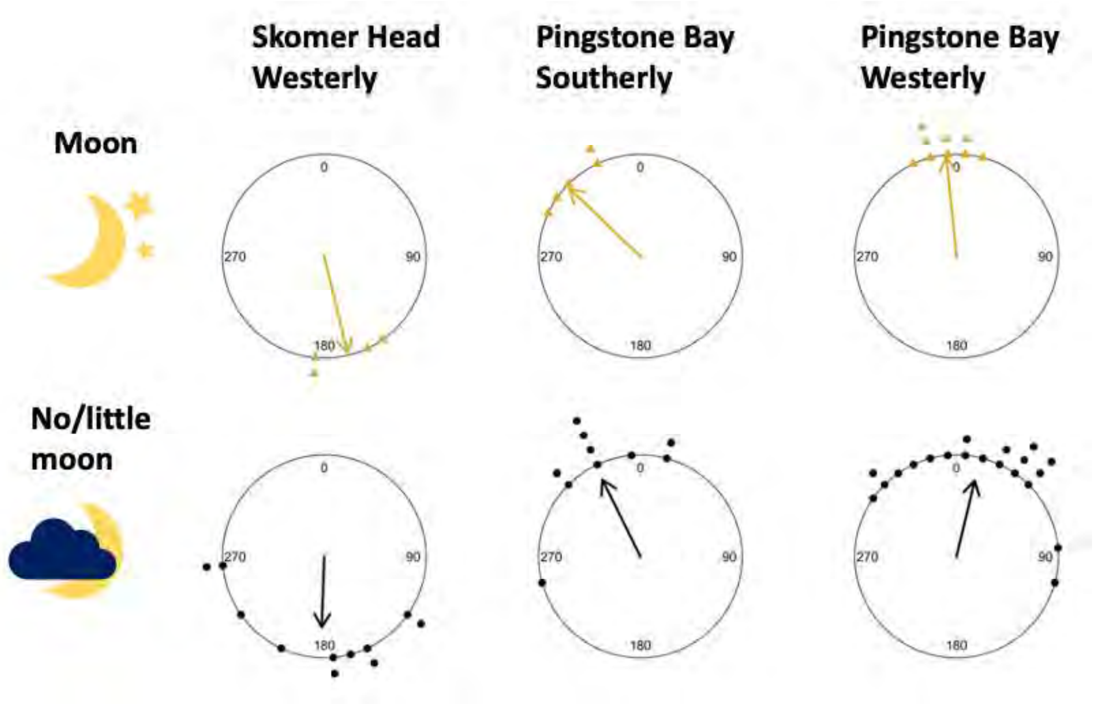


Figure S3.2. Circular graphs showing vanishing bearings of Manx shearwaters in westerly and southerly winds in Pigstone Bay and in westerly winds at Skomer Head. Each yellow triangle (moonlit) and black dot (moonless) indicates the vanishing bearing of one individual Manx shearwater. The arrows indicate mean vectors for each group. All graphs are relative to geographic north.

Chapter 4

The influence of light on the initial orientation of Manx shearwater fledglings

Martyna Syposz, Madeleine O'Connor, Oliver Padget, Natasha Gillies and Tim Guilford

ABSTRACT

Light is an important cue for orientation of many animals that are active during the night, and is used as a natural orientation cue for some animal neonates, such as sea turtles. Hence, artificial light pollution adjacent to nesting sites of such species can mean that these behavioural responses to light result in orientation which has negative fitness and survival consequences. Here, we hypothesise that the often fatal grounding of fledgling Procellariiform seabirds is a result of attraction towards light pollution, akin to the behaviour of hatchling turtles, in which the natural orientation cue of the brightness of the horizon, which would ordinarily direct them towards the safety of the sea, causes them to misorientate towards sources of artificial light. To test this hypothesis, we developed a novel assay using a circular arena to investigate the initial orientation of juvenile Manx shearwater (*Puffinus puffinus*) at their natal colony. We investigated the orientation of birds exposed to a torch (experiment 1), a bright horizon (experiment 2), as well as towards the sea without the use of visual cues (experiment 3). We successfully measured initial orientation of fledgling seabirds on the ground but found only limited evidence that the orientation is influenced by the brightness of the horizon or the location of the sea.

Understanding the mechanism of the attraction of seabirds towards artificial light could have an important conservation application, guiding actions targeted on limiting the numbers of affected birds. Thus, we recommend further studies helping understand the behaviour of fledgling Procellariiform seabirds.

INTRODUCTION

Assays investigating orientation in wild animals have widened our understanding of the intricacies of navigation behaviour, including the mechanism of bird migration (e.g. Emlen, 1975; Wiltschko and Wiltschko, 1975; Åkesson, 1993), the information required for homing behaviour in ants (e.g. Narendra, 2007a, 2007b), the cues directing dung ball rolling in diurnal and nocturnal dung beetles (e.g. Dacke *et al.*, 2013, 2019; Jundi *et al.*, 2014, 2015), and how hatchling turtles are able to reach the sea (e.g. Lohmann and Lohmann, 1994; Bourgeois *et al.*, 2009; Limpus and Kamrowski, 2013). Improvement in orientation assays (e.g. Bianco *et al.*, 2016; Cruz *et al.*, 2018) as well as the development of new techniques (e.g. Guilford *et al.*, 2011; Padget *et al.*, 2018) prompt new insight into animal behaviour.

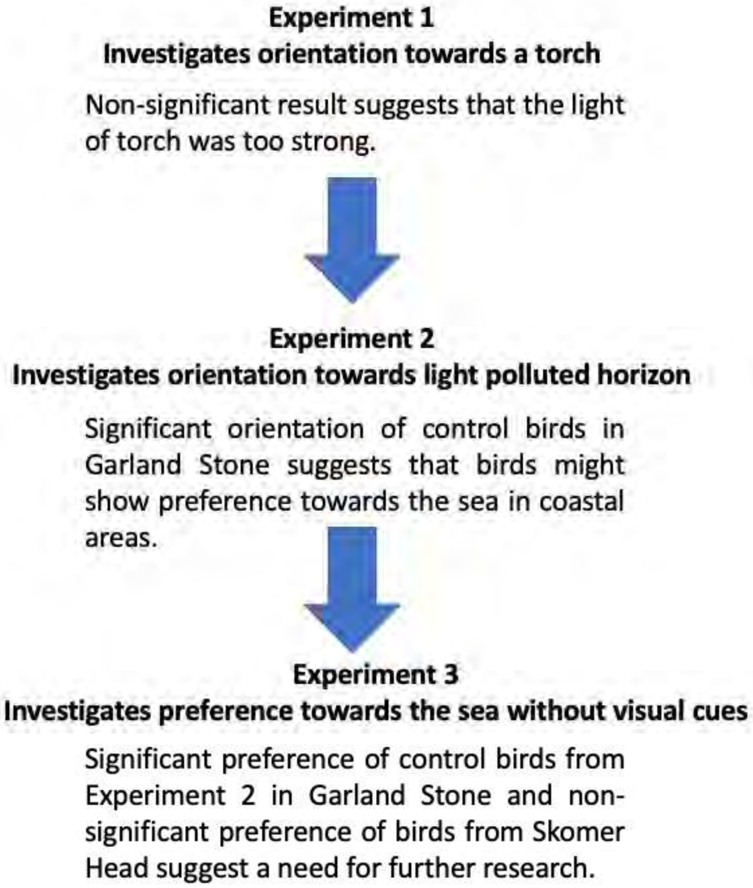
Assays examining the orientation of animals active during the night, for example, have shown that light from the stars and moon is important for their orientation (e.g. Emlen, 1975; Mrosovsky and Kingsmill, 1985; Dacke *et al.*, 2013). This raises concerns in places where natural levels of light at night are disrupted by light created by humans e.g. by streetlights, illuminated buildings, monuments or football pitches (Witherington and Martin, 2000; Rodríguez *et al.*, 2017; Van Doren *et al.*, 2017). The effect of light pollution on orientation has been especially well investigated in sea-finding behaviour of hatchling turtles (Carr and Ogren, 1960; Mrosovsky and Shettleworth, 1968; Lorne and Salmon, 2007; Karnad *et al.*, 2009; Rivas *et al.*, 2015). Once young turtles emerge from their nest during the night, they rapidly crawl towards the sea. Failure to progress quickly to the water may result in dehydration, exhaustion and increases the risk of predation

(Witherington and Martin, 2000). This important movement is guided by two simple cues: the brightness and elevation of the horizon (Tuxbury and Salmon, 2005), which works on the principle that the sea is situated lower than sand dunes and reflects more light than vegetation and sand. On beaches near to costal developments, the light intensity gradient created by brightness of the sea and darkness of the sand is disturbed. Often, artificial light pollution is brighter than the sea and thus, hatchling turtles orient towards the cities and towns where they can be entrapped between buildings, crushed by passing vehicles or depredated by cats or dogs (McFarlane, 1963; Salmon, 2006; Bourgeois *et al.*, 2009). Understanding the cues driving sea-finding behaviour of hatchling turtles has resulted in many well-informed conservation actions (Salmon, 2006; Deem *et al.*, 2007). The mechanism of attraction towards light pollution, however, remains still unexplored in most other species.

Burrow and crevice-nesting seabirds in the order Procellariformes appear to be similarly affected by coastal artificial light pollution. In this group of animals, young individuals are mainly affected by light, with fledglings representing 68 to 99% of grounded individuals (Rodríguez *et al.*, 2017). Young birds leave the nest at night and are then found close to brightly lit structures, including towns, cities (e.g. Ainley *et al.*, 2001; Le Corre *et al.*, 2002; Miles *et al.*, 2010; Rodríguez, Rodríguez and Lucas, 2012; Rodríguez *et al.*, 2014; Syposz *et al.*, 2018), but also boats and oil platforms (Ryan, 1991; Wiese *et al.*, 2001; Black, 2005; Merkel and Johansen, 2011; Glass and Ryan, 2013; Day *et al.*, 2015; Ronconi, Allard and Taylor, 2015) during their first movements towards the sea. As is the case for turtles, once they are trapped between buildings and structures, they are unable to safely return to sea without human intervention, leading to the phenomenon being termed ‘fallout’ or ‘grounding’ (Telfer *et al.*, 1987; Syposz *et al.*, 2018). There are many similar patterns between sea-finding in turtles and seabirds: in both, fewer animals are affected during the full moon (Salmon and Witherington, 1995; Bourgeois *et al.*, 2009; Miles *et al.*, 2010; Syposz *et al.*, 2018), and the phenomena are dependent on both the intensity (Reed, Sincock and Hailman, 1985; Rodríguez *et al.*, 2014; Rivas *et al.*, 2015; Rodríguez, Dann and Chiaradia, 2017) and wavelength (Salamolard *et al.*, 2001; Rivas *et al.*, 2015) of light. In seabirds, however, only limited research has explored the mechanistic basis of their movement towards artificial light (Rodríguez, Rodríguez and Negro, 2015).

The aim of this chapter is to (i) develop an assay to test orientation of fledgling seabirds on the ground, and (ii) investigate whether the fallout of Procellariiformes is a result of the same mechanism that drives turtles’ attraction to light. We propose that juvenile seabirds, on their maiden flight, orient towards an illuminated horizon, similarly to hatchling turtles (Tuxbury and Salmon, 2005). The initial orientation of fledglings could be directed towards the lowest and brightest part of the horizon as under natural conditions, this would ensure that they fly away from land, where they are vulnerable to predators, and towards the sea. Artificial light may trigger a similar response and cause them to ground in light polluted areas. In order to test this hypothesis, we designed three experiments to determine the drivers of initial orientation of juvenile seabirds on the ground at their natal colony.

We used Manx shearwaters (*Puffinus puffinus*) as the study species. As a medium sized Procellariiform seabird weighing around 400g, Manx shearwaters are unsuitable for testing in the Emlen funnel apparatus customary for passerines (Emlen, 1975). Instead, we designed a large, orientation arena for this species which could be deployed flexibly in the breeding colony itself. Arenas have similarly been used in experiments investigating the initial orientation of hatchling sea turtles (e.g. Rivas *et al.*, 2015; Cruz *et al.*, 2018) and the ball-rolling orientation behaviour of dung beetles (e.g. Dacke *et al.*, 2013, 2019). In this chapter, we develop techniques to study the initial orientation preference of fledgling Manx shearwaters, reporting the development process as a series of experiments, the design of each being inspired and improved based on the results of the previous experiment (Fig. 4.1). In the first two experiments we tested weather Manx shearwaters orientate towards a bright part of the arena lit by a torch (experiment 1), and the horizon lit by lights from ships (oil and gas tankers, experiment 2). In both of these experiments we predicted that fledgling Manx shearwaters would orientate towards the light. Results from our analysis suggested that seabirds might preferentially orientate towards the sea even in the absence of visual cues. Thus, we tested this hypothesis by running an additional test on control birds from experiment 2 and, to exclude the possibility of site-specific biases, by repeating the experiment at another site (experiment 3).



Experiment 1
Investigates orientation towards a torch

Non-significant result suggests that the light of torch was too strong.

Experiment 2
Investigates orientation towards light polluted horizon

Significant orientation of control birds in Garland Stone suggests that birds might show preference towards the sea in coastal areas.

Experiment 3
Investigates preference towards the sea without visual cues

Significant preference of control birds from Experiment 2 in Garland Stone and non-significant preference of birds from Skomer Head suggest a need for further research.

Figure 4.1 Chapter 4 consists of three experiments investigating orientation of young Manx shearwaters on the ground. The diagram shows a progression between the series of experiment, explaining which conclusions from the experiments lead to the design and hypothesis of the following experiment.

METHODS

Site and species

The experiments were conducted at four different sites on Skomer Island, Wales (51˚ 44’ N, 5˚ 17’ W; Fig. 4.2) between August 27th and September 21st, 2019. Manx shearwaters are burrow-nesting seabirds, which, while diurnal at sea, enter and leave their burrows only at night, possibly to avoid predation (Watanuki, 1986; Keitt, Tershy and Croll, 2004; Silva *et al.*, 2011).

Figure 4.2 A map with the location of Skomer Island (right top corner) and the locations of experiment 1 (South Park), experiment 2 (Farm and Garland Stone) and experiment 3 on Skomer Island (Garland Stone and Skomer Head, OpenStreetMap®, 2020).

At night, older Manx shearwater fledglings, similar to other burrow-nesting Procellariiformes*,* come out onto the surface to exercise their wings, build their flight muscles, and eventually fledge (Yoda, Shiozaki, *et al.*, 2017). On their maiden flight, fledglings are reported to ground in light polluted areas near to their nesting sites (Miles *et al.*, 2010; Syposz *et al.*, 2018), including the mainland coast of Wales (Anna Sutcliffe pers. comm.) and tankers anchored near Skomer Island (personal observation).

During these night-time excursions, we caught Manx shearwater fledglings and tested their orientation. In order to select birds that were ready to fledge, we chose individuals that had no obvious down feathers visible and a mass between 410-465g. The lower mass boundary was chosen to avoid selecting fledglings in abnormally poor condition, whereas the top mass boundary ensured that birds had not recently been fed by parents and were potentially ready to fledge (Brooke, 1990). No visible down feathers ensured those chosen individuals were fully developed (Perrins, 2014). A bird's capture location was marked with reflective tape or recorded in the GPS & Maps: Track Coordinates, Compass + Waypoints (©2kit consulting) app on a smartphone. All birds were ringed with a permanent, stainless-steel ring provided by the British Trust for Ornithology and, following the experiment, returned to their original collection point. The study was conducted after ethical approval by Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford's Local Ethical Review Process.

Design of the arena

For the experiments we used an arena designed specifically for Manx shearwaters (Fig. 4.3). The arena had a diameter of 5.6 meters and was situated on a flat area to avoid any confounding effects of slope (Supplementary material). An outer wall was constructed by installing 8 metal poles as fenceposts and stretching a piece of black polythene sheeting between them, from the ground up to a height of 1 meter. The outer barrier both prevented shearwaters from escaping and ensured that the background was visually uniform around the entire arena.

A second polythene fence with a diameter of 3.8 meters was constructed in the centre of the arena. A gap of 40-45 cm was left between the ground and the bottom of the polythene sheeting to allow birds to walk underneath. Every 15 degrees was marked on the sheet outside the inner fence to facilitate measuring the orientation of the bird.

In each experimental trial, fledgling Manx shearwaters were initially contained within a 40 x 40 x 15cm wooden ‘start’ box with mesh sides, which was placed in the centre of the arena. The bottom of the box was left open and the top of the box was secured to a 2m pole, so that it could be lifted off the bird from outside the arena. The bird was left in the box for 5 minutes to acclimatise to its surroundings. The box was then lifted, and the trial began, and fledglings were allowed to explore the arena freely. As soon as the bird passed under the inner fence, its leaving position was recorded as the bird’s orientation, together with the time elapsed since the box was lifted. If a bird did not pass the inner fence within 10 minutes, the trial was classified as NO EXIT. Each bird was used only once.

Birds were observed via night scopes by two researchers positioned opposite each other. They recorded the orientation of the bird, duration of the trial, and observed for any signs of distress (increased breathing, vocalisation). None of our birds showed signs of stress following the initial 5 minutes' acclimatisation.

Experiment 1

To test whether juvenile Manx shearwaters orient towards an artificially lit background, we used a standard torch, to create a concentrated light area within the arena (Fig. 4.3). The torch was covered with a Cokin® gel filter 210, which reduces light intensity two fold, without changing its colour. The torch faced downwards onto a white cloth (75cm x 50 cm), beyond the perimeter of the inner fence, but within the outer barrier, so that the spread of light was limited by outer barrier. The torch was positioned at one of two different locations in the arena, 120 degrees away from each other (torch position I and II, Fig. 4.3). For the control treatment, no torch light was used, but all the other equipment (pole, torch, cloth) was placed in the experimental position. Analyses for all the experiments were conducted in `R` (version 1.1.456, R Core Team 2018) using the package '`circular`' (Lund and Agostinelli, 2017). A Rayleigh test was conducted to test if all the birds, as well as separately the control and experimental birds were significantly oriented, and a Watson-wheeler test was used to investigate differences in orientation between the control and experimental groups.

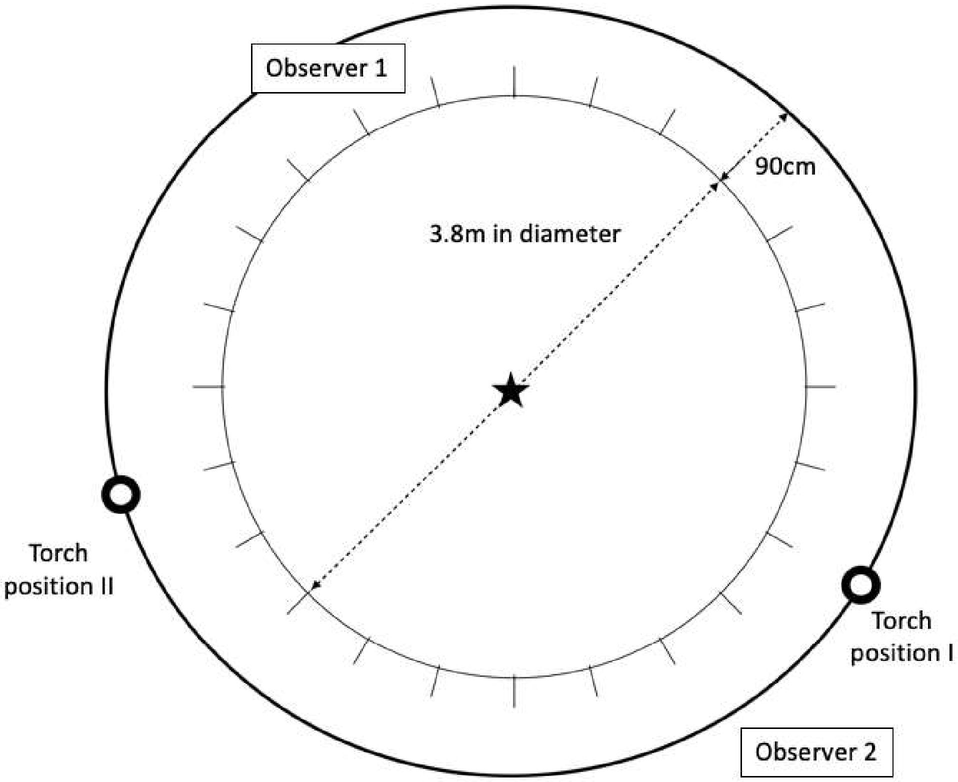


Figure 4.3 The arena used for experiment 1, which tested the orientation of juvenile Manx shearwaters in response to torchlight. The graph shows the outline of the inner fence (thin circular line) and outer barrier (thick circular line), the positions of the two observers, two possible positions of a torch and the 15 degrees markers that were made on the sheet outside the inner fence (the lines around the inner circle). The inner fence, 3.8m in diameter, and outer barrier, 5.6 in diameter, were made from black polythene sheeting attached to the ground by 8 metal stakes for fences. The outer barrier had 1m sheeting from the ground, whereas the inner fence had 40-45cm gap between the ground and the bottom of the sheeting, allowing the birds to walk underneath it.

Experiment 2

Experiment 2 was undertaken at two locations on Skomer Island: the Farm and Garland Stone (Fig 4.2). The same arena as for experiment 1 was used (Fig. 4.3), but this time relevant 45° angular sections of the outer arena were opened to provide a bird with view of the sea (segment Sea, Fig 4.4), the sea with a tanker (segment Tanker), and two different sections of land (segments Land X and Land Y). We had two segments of view with the Land to check if there was no bias towards one of them. During the experiment, we covered two of the open segments to provide a bird with a choice between two of the four possible views. For the analysis of results, our two Land views were combined, to give four experimental treatments: Land – Land, Sea – Land, Tanker – Land, and Tanker – Sea. For the control treatment we covered all the four sections of the outer barrier. The order in which treatments were arranged was selected using a constrained randomised design; each treatment was repeated twice in a row (for different birds) before moving on to the next one.

We first tested if birds in each treatment are oriented using Rayleigh test. To determine whether Manx shearwaters orient towards the brightest part of the horizon available to them, the angle between the middle of the brightest part and the bird's orientation was calculated. We also calculated for each treatment the actual difference between the Rayleigh statistic of experimental and control birds. We then randomised the treatment identity (experimental or control) of each bird 10 000 times and calculated the global difference between the Rayleigh statistics of experimental and control treatments for each run.

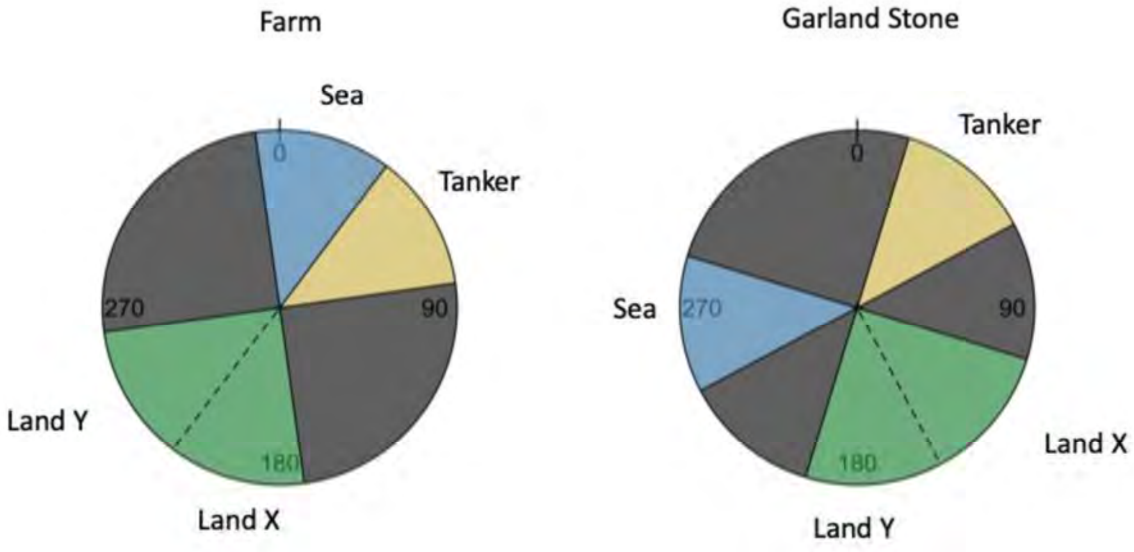


Figure 4.4 The division of the arena into four different segments (Tanker, Sea, Land X, Land Y) used for experiment 2 at the Farm (left) and Garland Stone (right). The grey sections show segments of outer barrier closed during all the treatments. Orientations are in relation to geographical North.

Experiment 3

To assess whether juvenile Manx shearwaters preferentially orient towards the sea in the absence of visual cues, we used half of our control data from experiment 2 (Garland Stone). This part of experiment 2 was conducted close to the sea and thus was relevant for the hypothesis of experiment 3. Additionally, we set up an arena at Skomer Head (Fig. 4.2) and used the same method as for the controls for experiment 2 by keeping the outer barrier closed.

Before the experiment, we measured the degrees at which the sea and land were visible from the middle of the arena without the outer barrier. The sea was visible from 242 to 77° at Garland Stone and 203 to 306° at Skomer Head, constituting 195° and 103° segment of the circle respectively (Fig. 4.6). A bird was sea-oriented if its orientation was within this segment and land-oriented if its orientation was in any other direction. A Chi-square test was used to compare birds that oriented towards the sea and land.

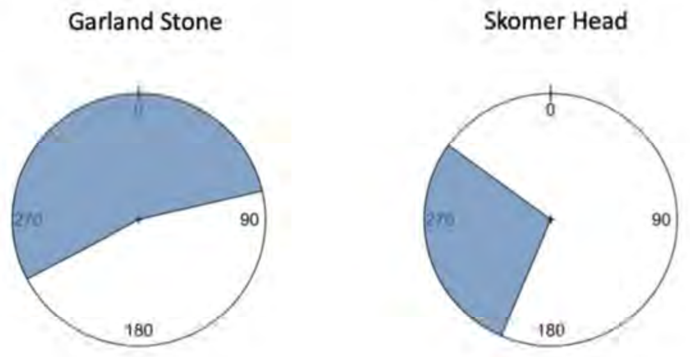


Figure 4.6 The representation of the sea visible from the middle of the arena in the Garland Stone (left; 242 to 77°), and Skomer Head trials (right; 203 to 306°). During the experiment the view of the sea was blocked with the outer barrier. Orientations are in relation to geographical North.

Meteorological data

Meteorological data including cloud cover, sky luminosity, wind direction and speed were collected at least every two hours during the experiment. An observer assessed the cloud cover on an nine-point scale (0 oktas being clear sky, 8 - a full cloud cover and 9 - sky obstructed by fog or other meteorogical phenomena). The sky luminosity was measured using a Sky Quality Meter (SQM) by Unihedron. The SQM measures the quality of the sky in magnitudes per square arc second (mag arcs^{-2}). Higher values indicate darker, thus better-quality sky, whereas lower values indicate brighter sky, possibly polluted with light (see Kyba *et al.*, 2011). The wind direction, in eight compass divisions, as well as average and maximum wind speed over a minute were measured by a handheld Vaavud anemometer (Vaavud ApS, Copenhagen S, Denmark). All experiments took place after nautical twilight to avoid any influence from sun glare.

RESULTS AND DISCUSSION

Experiment 1

48 birds were used in experiment 1, seven of which were classified as NO EXIT, leaving 41 for analysis (20 experimental: 10 torch position I, 10 torch position II; 21 control: 11 torch position I, 10 torch position II). The mass of collected birds was 415-465g (mean 439.5g; median 440g), and so it was considered that all birds were likely to be either attempting to fledge or very close to fledging. The duration of trials (time before birds exited the arena) varied between 5 and 540 seconds (mean = 161 sec; median = 90 sec). All trials were undertaken when the moon was below the horizon. Cloud covered varied between 0 and 8 (median = 3) and wind speed between and 1 and 7 m/s (median = 4 m/s). The wind directions were from NW, SW and W.

We found no significant orientation in control (mean = 195°, Rayleigh test: Rayleigh statistic = 0.156, p-value = 0.605), experimental treatments (mean = 186°, Rayleigh test: Rayleigh statistic = 0.344, p-value = 0.093), nor when we pooled both of these results together (mean = 188°, Rayleigh test: Rayleigh statistic = 0.247, p-value = 0.081). Furthermore, the Watson-Wheeler test confirmed no difference between experimental and control treatments (Watson-Wheeler test: W = 2, df = 2, p-value = 0.377, Fig. 4.7). These results suggest that Manx shearwaters do not preferentially orient towards torch light. However, it is possible that this outcome reflect issues with the experimental design: for example, the influence of the torch light may have been disrupted by the smell and movement of the cloth or shadows cast on the arena walls. We suggest, however, that this result was most likely due to brightness of the torch itself. The light intensity of the torch was much stronger than that of a horizon that seabirds are normally exposed to (with the SQM, we recorded a value of 12.5 for the torch, whereas we never measured below 19.2 for the sea). Possibly this light is stronger than any cues that seabirds might have been exposed to and this is why the light did not trigger an orientation response. Therefore, we decided to conduct an experiment using a light pollution stimulus that seabirds are known to be susceptible to; that generated by anchored ships (experiment 2; Black, 2005; Glass and Ryan, 2013; Merkel and Johansen, 2011; Ryan, 1991).

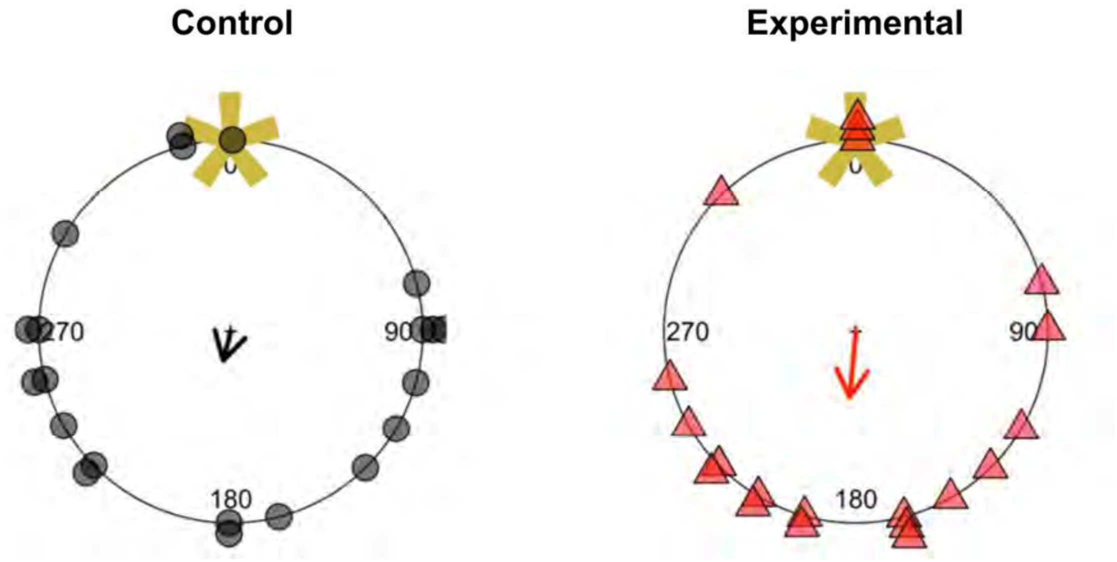


Figure 4.7. Circular plots illustrating the orientation of control (left, black circles) and the experimental (right, red triangles) birds from experiment 1. The arrow indicates the mean orientation of the group and the arrow's length corresponds to their Rayleigh value. Orientation is given relative to the position of the torch (yellow star).

Experiment 2

148 birds were collected for use in experiment 2, of which 19 were classified as NO EXIT, leaving 129 birds for analysis (Farm: 79, Garland Stone: 50). The mass of birds was 410-465g (mean 431.6g; median 430g). The duration of trials varied between 3 and 595 seconds (mean 164 sec; median 114 sec). The experiment was undertaken over 4 days at Garland Stone and 7 days at the Farm. SQM varied between 15.98 and 22.2 mag arcs^{-2} (median = 19.11 mag arcs^{-2}), and cloud cover measurements varied between 0 and 8 (median = 2). The wind direction was constantly changing over the course of the experiment, and its speed varied between 2 and 6 m/s (median = 2 m/s). In another study (O'Connor, 2020), we tested whether there was an influence of pick-up location on orientation of Manx shearwaters and we found no evidence of an interaction. In experiment 2, we found that birds were significantly oriented in Sea – Tanker treatments at both locations, as well as control birds at the Garland Stone (Table 4.1). Furthermore, we found no significant difference in orientation between control and experimental fledglings except from one treatment (Fig. 4.8; Table 4.1). At the farm, we observed a significant difference from control orientation of experimental birds to the Sea – Tanker treatment (premutation test, iterations = 10000, $p = 0.019$). Those birds were significantly oriented towards the Tanker segment (9° relative to brightest point; Rayleigh test: Rayleigh statistic = 0.7, p value < 0.001).

Birds in the Land-Land treatment showed no significant orientation which is consistent with behaviour of hatchling turtles. Hatchling turtles lack better than random orientation preference in dense vegetation (Godfrey and Barreto, 1995). Similarly, when we presented Manx shearwaters with only a view of land (Land-Land treatment), their orientation was random. It has been proposed that sea-finding is disturbed in turtles when there is not enough difference between intensity of the parts of the horizon (Godfrey and Barreto, 1995). This could be also true for orientation of Manx shearwaters on the ground.

Inadequate difference in the photic gradient of the horizon could explain the lack of difference in orientation between control and all the other non-significant pairings (Tanker – Sea at the Garland Stone, Sea – Land and Tanker – Land treatments). Alternatively, the orientation of Manx shearwaters could be driven by a combination between intensity of the horizon and the wideness of the view that they are exposed to. We exposed them to only 45º of horizon with the sea or sea with a tanker, which might have been insufficient to elicit the orientation response. This hypothesis is supported by our only significant result where seabirds were exposed to 90º of horizon. Manx shearwaters in the Sea – Tanker treatment at the Farm orientated towards the segment of the arena with the view of tankers. However, this provides only limited evidence that seabirds might be oriented towards light pollution when they are already on the ground as we were unable to replicate this result at the Garland Stone. Control birds at the Garland Stone showed a significant orientation, and thus the experimental treatment Sea - Tanker was not different from the control, even though their mean orientation was directed towards tankers (24º relative to brightest point). The significant orientation of control birds in Garland Stone led to experiment 3, where we tested whether Manx shearwaters that are close to the coast might be oriented towards sea without visual cues.

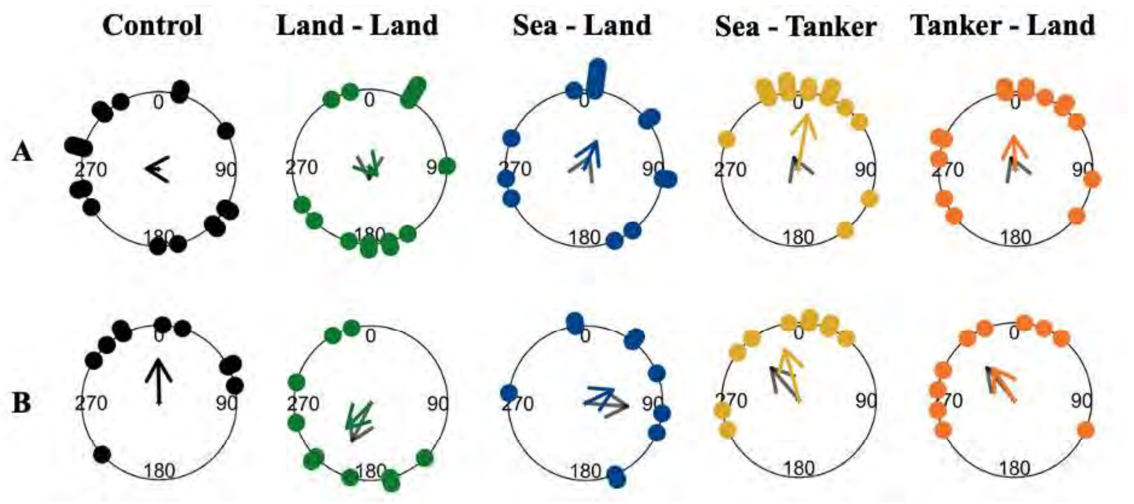


Figure 4.8 Circular plots illustrating the orientation of birds in experiment 2 (**A**: Farm, **B**: Garland Stone). For the experimental group, orientations are shown relative to the middle of the brightest part of the horizon, while in the control treatment they are shown relative to north. The grey arrow in experimental treatments shows the orientation of control birds for comparison. For detailed statistics, see Table 4.1.

Table 4.1 Table showing the sample size, the mean angle to the brightest point (for control all angles are compass-headings), results of Rayleigh test and the results of randomisation of difference between Rayleigh statistic of control and experimental birds for experiment 2. ***P < 0.001; **P < 0.01; *P < 0.05.

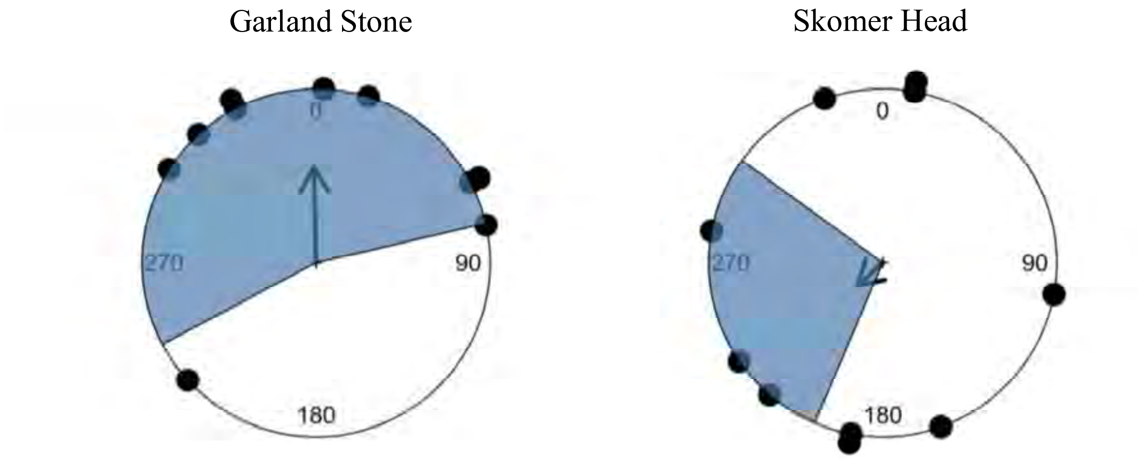
Treatment	Sample size	Mean angle to the brightest point (0-180)	Rayleigh statistic (0-1)	Rayleigh test p-value	Permutation test p-value
Farm					
Control	18	88 (to North)	0.157	0.649	
Land, Land	15	139	0.147	0.731	0.701
Sea, Land	15	24	0.369	0.13	0.26
Sea, Tanker	16	9	0.7	<0.001***	0.019 **
Tanker, Land	15	3	0.41	0.071	0.192
Garland Stone					
Control	10	108 (to North)	0.547	0.046*	
Land, Land	10	135	0.45	0.135	0.715
Sea, Land	10	64	0.396	0.212	0.768
Sea, Tanker	10	24	0.675	0.007**	0.296
Tanker, Land	10	35	0.49	0.088	0.679

Experiment 3

For the analysis of experiment 3, we used data collected from our control birds in experiment 2 alongside the results from 10 birds used in an experiment conducted at Skomer Head (out of 11 birds used, where 1 was NO EXIT). The mass of birds was 410-450g (mean 427g; median 427g). The duration of trials varied between 20 and 582 seconds (mean 211 sec; median 125 sec).

We tested birds at Skomer Head on a single night with no cloud cover, where SQM measurements varied between 18.97 and 21.25 and when there was a very light wind from NE (min = 0m/s, max = 3m/s, median = 2m/s). The birds from the Garland Stone site were tested on four days with varied cloud cover (min = 0, max = 8, median = 1), SQM measurements (min = 15.98, max = 19.78, median = 17.89) and strong E, NE, N and W winds (min = 2m/s, max = 6m/s, median =4m/s).

A chi-square test of goodness-of-fit was performed to determine whether orientation towards the sea or land was preferred. Manx shearwaters at the Garland Stone were more likely to go towards the sea than expected (chi-square test, X^2 = 5.172, df = 2, n= 10, p value = 0.028), but birds at Skomer Head did not (chi-square test, X^2 = 0.0094, df = 2, n= 10, p value = 1, Fig. 4.9). These results suggest that we found weak evidence for orientation of Manx shearwaters towards the sea without visual cues. The reason for the difference in orientation of Manx shearwaters in Skomer Head and Garland Stone might be difference in site-specific and environmental variables. We undertook the experiment at Skomer Head only under very calm weather conditions. Almost no wind meant that potential orientation cues such as olfactory (smell of the sea) or acoustic (sound of waves crashing on rocks) were less available to Manx shearwaters at Skomer Head. Furthermore, there was a difference in the distance from the sea in these two locations. The arena was located closer to the sea at the Garland Stone (~90m) than at Skomer Head (~120m), potentially strengthening the orientation cues available to direct birds towards the sea. Therefore, future experiments should be repeated under different weather conditions, in more locations and they should consider odour and sound measurements to determine whether Procellariiform fledglings are capable of orienting towards the sea without visual cues.


Garland Stone

Skomer Head

Figure 4.9 Circular plots representing orientation of control birds at Garland Stone (left) and Skomer Head (right) for experiment 3. The shaded blue area is a representation of the sea visible from the middle of the arena. The orientations are in relation to geographical North.

CONCLUSION

We successfully developed a novel assay which makes use of an arena set-up that enables testing orientation of juvenile seabirds on the ground. This technique allowed us to find limited and weak evidence for Manx shearwater orientation towards a light polluted horizon and preference towards the sea without visual cues, which hints that the orientations measured using our assay were biologically meaningful. We suggest interpreting these results with caution and conclude that determining the drivers of young seabirds' orientation on the ground requires more research. Further studies could include repeating the experiments at more sites and under varied weather conditions.

This assay could be used to answer other orientation related questions in fledgling seabirds, including the effect of slope of ground or topography of the viewed horizon on orientation. Our technique could help to determine the cues that drive adult seabirds' orientation when they head out to sea, and when they come back to the colony in search of their burrow.

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SUPPLEMENTARY MATERIAL

Calculating a slope of the ground

To ensure that the steepness of the ground does not influence the orientation of Manx shearwaters in our experiments, we calculated the steepness using an inclinometer. We measured a steepness by putting the inclinometer on a 2m-long pole positioned in the middle of the arena. Four measurements were taken 45º from each other.

The results showed that the mean steepness in the arena in Farm was 1º, in Skomer head was 2.2º and in Garland Stone it was 2.4º. These measurements showed that the steepness inside the arena at these three locations was negligible.

Chapter 5

Does transition to LED streetlamps reduce grounding of a nocturnal seabird? A citizen-science study.

Martyna Syposz, Natasha Gillies, Oliver Padget, Annette L. Fayet, Fabrizio Manco, Martin Carty and Tim Guilford

ABSTRACT

Light-emitting diodes (LED) have become an energy-efficient and long-lasting competitor to traditionally used sodium pressure and mercury vapor bulbs. However, the changes in light intensity and composition associated with recent switches to LEDs worldwide as an outdoor light source may affect the circadian rhythms and behaviour of many species of wild animals.

Here, in a ten-year citizen science study across a coastal village in northwest Scotland, Mallaig, we investigated whether the transition to LED lighting streetlamps affected the number of grounded Manx shearwaters (*Puffinus puffinus*). These nocturnal seabirds are vulnerable to grounding and often struggle to take to sea again without human intervention.

The number of Manx shearwaters grounded in the village was measured between 2009 and 2019. We measured light intensity under each lamppost, as well as at the intersection of 50m grid covering the village before and after the transition to LED streetlamps in 2015-2016. Although we found an overall decrease in the light intensity, the transition to LEDs was not associated with a decrease in the number of grounded Manx shearwaters. We suggest that this is most likely caused by a different spectrum composition used in LED lights, especially the blue part of the spectrum, and recommend that future transitions to LED lights in places where birds ground should consider using bulbs with spectra focused in red and yellow ranges.

INTRODUCTION

With increasing urbanisation, nocturnal light pollution has soared globally in the last century, changing the nocturnal landscape and affecting wildlife (Hölker *et al.*, 2010; Gaston *et al.*, 2014; Falchi *et al.*, 2016). This issue is not restricted to land, and although oceans remain largely free from artificial light at night, light pollution along the coast has increased due to the presence of watercraft and coastal developments (Davies *et al.*, 2014). This is known to affect many marine animals including seabirds (Salmon, 2003; Longcore and Rich, 2004; Rodríguez *et al.*, 2017). In particular, Procellariiform seabirds are widely reported to ground in light polluted areas near to their nesting sites, where they are not able to take off again due to their forward-heavy anatomy which is adapted to life at sea. Large-scale fallout events can cause declines in seabird populations (Day, Cooper and Telfer, 2003; Fontaine, Gimenez and Bried, 2011; Rodríguez, Rodríguez and Lucas, 2012). Changing the nature of light pollution in coastal areas near seabird colonies (for example by changing the intensity, type or wavelength of bulbs) has been proposed as a potential conservation measure to reduce seabird groundings (Rodríguez *et al.*, 2017). However, how different types of light bulbs affect seabird grounding remains poorly understood and should be investigated first before making conservation recommendations.

The recent development of commercially available, energy-efficient and long-lasting light-emitting diodes (LED) has resulted in a rapid change from pressure sodium lamps and mercury vapor lamps to LED for street lights (Hecht, 2016; Pagden, Ngahane and Amin, 2020). The wavelength composition of pressure sodium lamps concentrates in the yellow-to-orange region of the visible spectrum, whereas mercury vapor lamps emit a broad-spectrum, including a large amount of UV radiation (Owens and Lewis, 2018). LED lights are available in a range of spectra and intensity (Boyce, Fotios and Richards, 2009; Dudley, Erkintalo and Genty, 2015), but typically have peaks in the blue and green part of the spectrum (Gaston and Holt, 2018). Blue wavelengths have been shown to have an effect on the circadian rhythms and behaviour of many species in a range of taxa (Lockley, Brainard and Czeisler, 2003; Evans *et al.*, 2007; P. Wilson *et al.*, 2018; Fischer, Gangloff and Creed, 2019; Timothy, Samiala and Okrikata, 2019; Williams *et al.*, 2019). Thus, introducing LED bulbs in streetlamps has aroused concern and driven research efforts into their effects (Longcore *et al.*, 2018; Owens and Lewis, 2018). However, this is an emerging field and many outstanding questions remain.

In seabirds, a study by Rodríguez, Dann and Chiaradia (2017) reported that high pressure sodium lights showed the lowest percentage of collected grounded short-tailed shearwaters (*Ardenna tenuirostris)* compared to LED lights and metal halide lights. For tropical shearwaters (*Puffinus bailloni*), the spectrum of light has been shown to have an influence on fallout, with red and yellow lights resulting in fewer groundings than green and blue (Salamolard *et al.*, 2007). Furthermore, changing from white broadband to red and green lights was associated with a reduction in grounding rates for seabirds in Chile (reported in Rodríguez, Holmes, et al., 2017). Besides the spectrum of light, intensity has also been reported to play an important role on seabird grounding. Covering and turning off lamps, as well as limiting the usage of light, reduces fallout of seabirds in otherwise well-lit areas (Reed, Sincock and Hailman, 1985; Miles *et al.*, 2010; Glass and Ryan, 2013; Rodríguez *et al.*, 2014). Spatial models also generally show positive relationships between light pollution levels and fallout distribution (Troy, Holmes and Green, 2011; Rodrigues *et al.*, 2012; Troy *et al.*, 2013). However, the effect of switching from sodium bulbs to LED streetlights, a common change in western urban areas (Hecht, 2016), on seabird grounding remains unclear.

Here we address this question using a Scottish village prone to seabird groundings as a case study. The village of Mallaig, located 27 km away from the second largest colony of Manx shearwaters (*Puffinus puffinus*) in the world, the Isle of Rum, experiences high numbers of seabird groundings each year (Syposz *et al.*, 2018). Juveniles start fledging in late August and appear to be particularly badly affected by light pollution, with hundreds grounding in the village by September. If a grounded bird is trapped between buildings or in vegetation, it may fall victim to predation, cars, dehydration or starvation (Ainley *et al.*, 2001; Le Corre *et al.*, 2002; Rodríguez *et al.*, 2014). In Mallaig, volunteers rescue hundreds of Manx shearwaters each year, capturing them at night and releasing them at sea the next day. Since 2009, they have recorded the numbers of birds grounded each night. In 2015 and 2016, for economic reasons, the bulbs in the village's streetlights were changed from low-pressure sodium and high-pressure sodium to neutral white LED, providing a unique opportunity to investigate whether this transition had an effect on the number of grounded Manx shearwaters. We investigated the change in light intensity across the village and hypothesised that if the change to LED lights resulted in lower light intensity, this should be associated with a decrease in the number of grounded shearwaters, whereas higher light intensity would be associated with an increase in groundings (Reed, Sincock and Hailman, 1985; Troy, Holmes and Green, 2011; Rodrigues *et al.*, 2012; Glass and Ryan, 2013; Troy *et al.*, 2013).

METHODS

Study site, species and collection of grounded shearwaters

Mallaig (57° 0′ 14.57″ N, 5° 49′ 52.36″ W) is located 27 km to the east from the second largest colony of Manx shearwaters globally, on the Isle of Rùm (Fig. 5.1), home to around 76,000 pairs (Murray *et al.*, 2003). There are two more small colonies of Manx shearwaters near Mallaig, on island of Canna (12-15 breeding pairs, B. Swann, unpublish data) and Eigg (50-150 breeding pairs, J. Chester, pers. comm.).

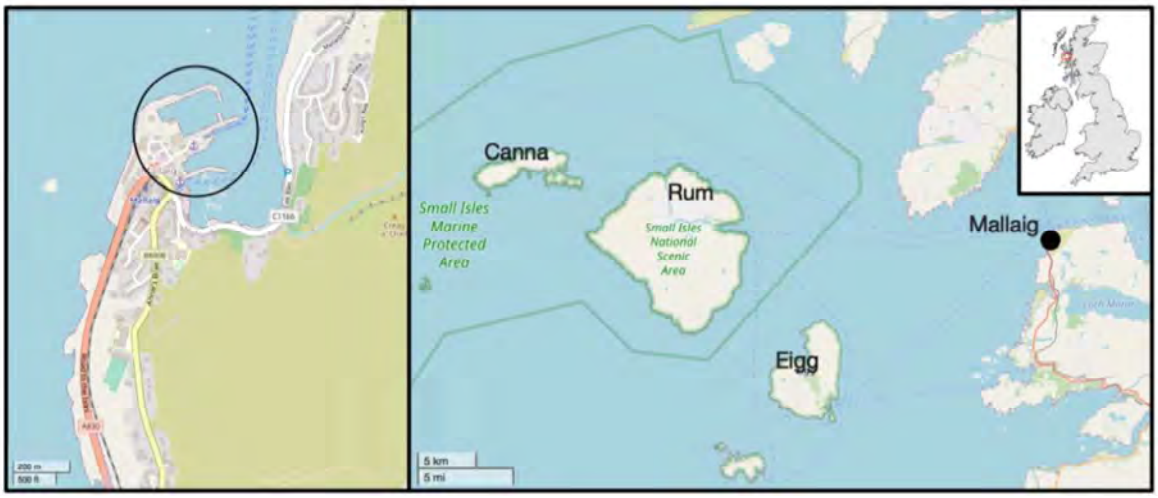

Figure 5.1. Map and location of the study site, Mallaig (OpenStreetMap®, 2020b) and nearby Manx shearwater colonies on islands of Rum, Eigg and Canna (OpenStreetMap®, 2020c). The area outlined with the black circle shows the harbour where the survey was undertaken.

Manx shearwaters are pelagic birds belonging to the order Procellariiformes. They spend most of their life at sea in the South Atlantic and come to breed on Northern Hemisphere islands, mainly in the UK, between April and September. Manx shearwaters nest in underground burrows which are visited only at night, probably to avoid predation (Watanuki, 1986; Keitt, Tershy and Croll, 2004; Silva *et al.*, 2011). Similarly, their offspring fledge at night to undertake their maiden flight to sea.

On the Isle of Rùm, the fledgling period starts around the end of August and ends in early October, coinciding with the time when most shearwaters are found grounded in Mallaig. Data on their grounding has been collected since 2009 by a local volunteer, who systematically patrols the harbour every night of September (circled area, Fig. 5.1). The searches are undertaken at this hour as the highest fledging activity, and therefore fallout, is expected 1 to 4 hours after nightfall (Reed, Sincock and Hailman, 1985; Rodríguez *et al.*, 2015). All search patrols are covered on foot with a very bright handheld torch that allows searching in crevices, under cars and in between objects. Rescue operations are often facilitated by the local community and volunteers. All collected birds are handled by the project founder (MC), who keeps them in well-ventilated boxes for the night. Every morning at 10:00 BST, the rescued birds are ringed and weighed, and the location at which they were found noted (as a description of nearest building or landmark).

Light measurement

The streetlamps in Mallaig were changed from sodium to LED bulbs in two phases in July/August 2015 and the same months in 2016. Light measurements were collected between the 4th and 24th of September 2014 and the 6th-15th August 2017. The light intensity in LUX was measured by placing a light meter (DT - 1301, CEM) on the ground. The measurements were taken under each streetlamp and at an intersection of a previously computed 50m grid covering Mallaig. Each measurement collected in a 50m grid was repeated three times and an average taken.

Light intensity maps (Fig. 5.2) were generated using the collected light intensity data points. To create an output layer, we used Inverse Distance Weighting (IDW) Interpolation from the package '`gstat`' (Pebesma, 2004) in `R` (version 1.1.456, R Core Team 2018). IDW is based on the principle that values decrease with distance from a created point. Finally, a map of differences in light intensity between 2014 and 2017 was created by subtracting the modelled light intensity variables from IDW maps.

Environmental variables

As fallout in seabirds is known to be affected by environmental factors (review: Rodríguez, Holmes, et al., 2017), we also controlled for the effects of moon phase, year, wind direction and speed, as well as visibility in our model to account for their effect on the number of grounded Manx shearwaters (Syposz *et al.*, 2018). To investigate the influence of environmental variables, hourly measurements of cloud cover, visibility, wind direction and wind speed were taken from a weather station in South Uist Range (Fig. S5.1, Table S5.1, supplementary material) for the entire survey period. For the purpose of modelling, we took an average between 22:00 BST and 01:00 BST as this is when most groundings occur.

Moonlight illuminance was also calculated for every hour using the method developed by Austin *et al.* (1976), implemented in moonlight Fortran software. This method includes a number of astronomical factors resulting in a realistic expression of moon brightness as perceived on the earth. Moon brightness is presented relative to the full moon at the zenith (for details see Rubolini et al., 2015). Next, we multiplied the calculated moon brightness by a number between 0.5 (full cloud cover) and 1 (clear sky), representing the proportion of cloud coverage. Then the average for each day was taken between 22:00 and 01:00. Finally, we rescaled the moon scale to an arbitrary 0-100% scale between minimum and maximum of the values.

Data analysis

To test whether the change in streetlamps bulbs is an important variable in predicting the number of grounded Manx shearwaters, we used the '`randomForest`' package in `R` to construct a random forest classification model (500 trees, Liaw and Wiener, 2002) with updated data from our previous paper (Syposz *et al.*, 2018). Although we had a descriptive location where birds were found and the light level per 50m grid, we decided not to investigate groundings per grid cell as the work effort was not systematic around the village. Instead we collated all the groundings for each night of September. Then, the number was predicted based on environmental variables, the factor variable of year and a factor variable presenting the change of bulb, where years prior to the change in bulb (2009-2014) were labelled "Before transition to LED", and after the change (2016 – 2019) labelled "After transition to LED". 2015 was excluded, because work on changing the bulbs was ongoing. We also created a variable from a random uniform distribution ('random'). We assessed the relative contribution of other variables in the model by comparing their importance to the random term (Eguchi *et al.*, 2017). To identify the relative importance of predictors, we used the basic residual sum of squares scores produced by the '`randomForest`' package (Wiener, 2003). Partial dependence plots of relationships between different variables and predicted number of grounded birds are located in Fig. S5.2 (supplementary material). Finally, we investigated the accuracy of the model by performing a correlation test between the observed and predicted number of collected birds. Additionally, we ran the same model including only the data from the systematically surveyed area (Fig. S5.3, supplementary material). The fact that our results were identical in the systematically surveyed and opportunistically surveyed areas suggests that our findings are not due to variations in effort.

RESULTS

Light measurement

According to the IDW model, overall light intensity in Mallaig decreased by 2681 LUX between 2014 and 2017 (from 92042 to 89361 LUX). The decrease, however, was not consistent across the village (Fig. 5.2). The highest decrease in light intensity was observed around the harbour (area outlined by black line, Fig. 5.2). However, a notable increase in light was observed in the centre of Mallaig where a new restaurant and marina were built. New streetlights were also established on Mallaigvaig road, in the north of Mallaig.

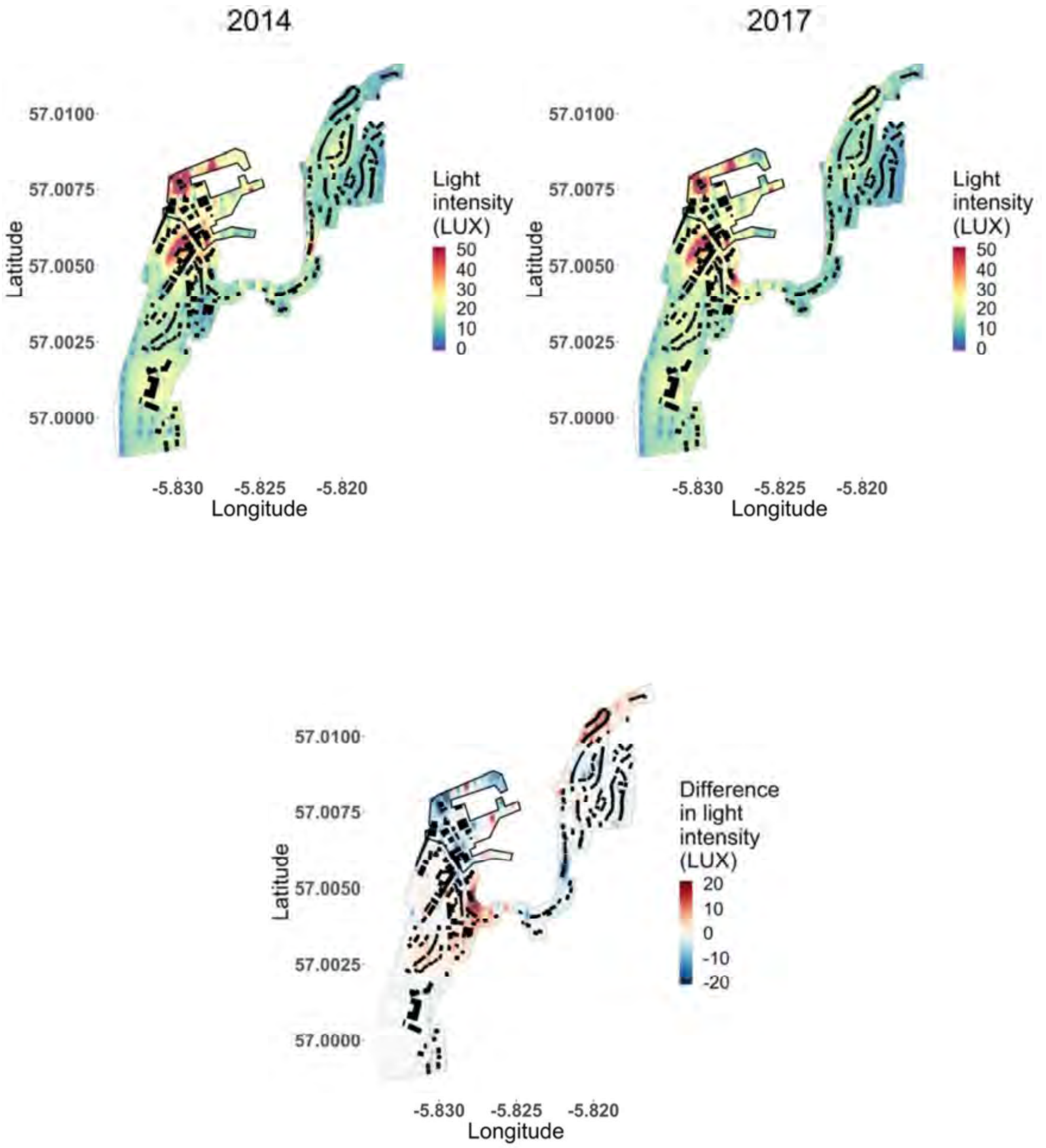

Figure 5.2. The village of Mallaig with light intensity measured in LUX in 2014 (top left), 2017 (top right, LED bulbs) and the difference between light intensity in those years (bottom). The area outlined with the black line shows the harbour.

Predictors of grounding

The random forest classification model explained 39.49% of the variance, showing that moon illuminance and year were the most important variables contributing to the model (Fig. 5.3a). These were followed by visibility, wind speed and wind direction. Grounding were exceptionally high in 2012 and 2018 (Fig. 5.3c). The change in bulb type had a smaller contribution to the model than the random variable suggesting that it did not affect the number of grounded birds (Fig. 5.3b). The predicted numbers of grounded Manx shearwaters were significantly correlated with the observed numbers ($p < 0.001$, $t = 12.827$, $df = 290$, $R^2 = 0.6016$), suggesting strong model performance. Partial dependence plots (Fig. S5.2, supplementary material) indicate that low moon illuminance results in higher numbers of grounded birds, low and high values of visibility and wind speed predict greater fallout, and, to a lesser extent, westerly and north-westerly winds contribute to a higher frequency of groundings.

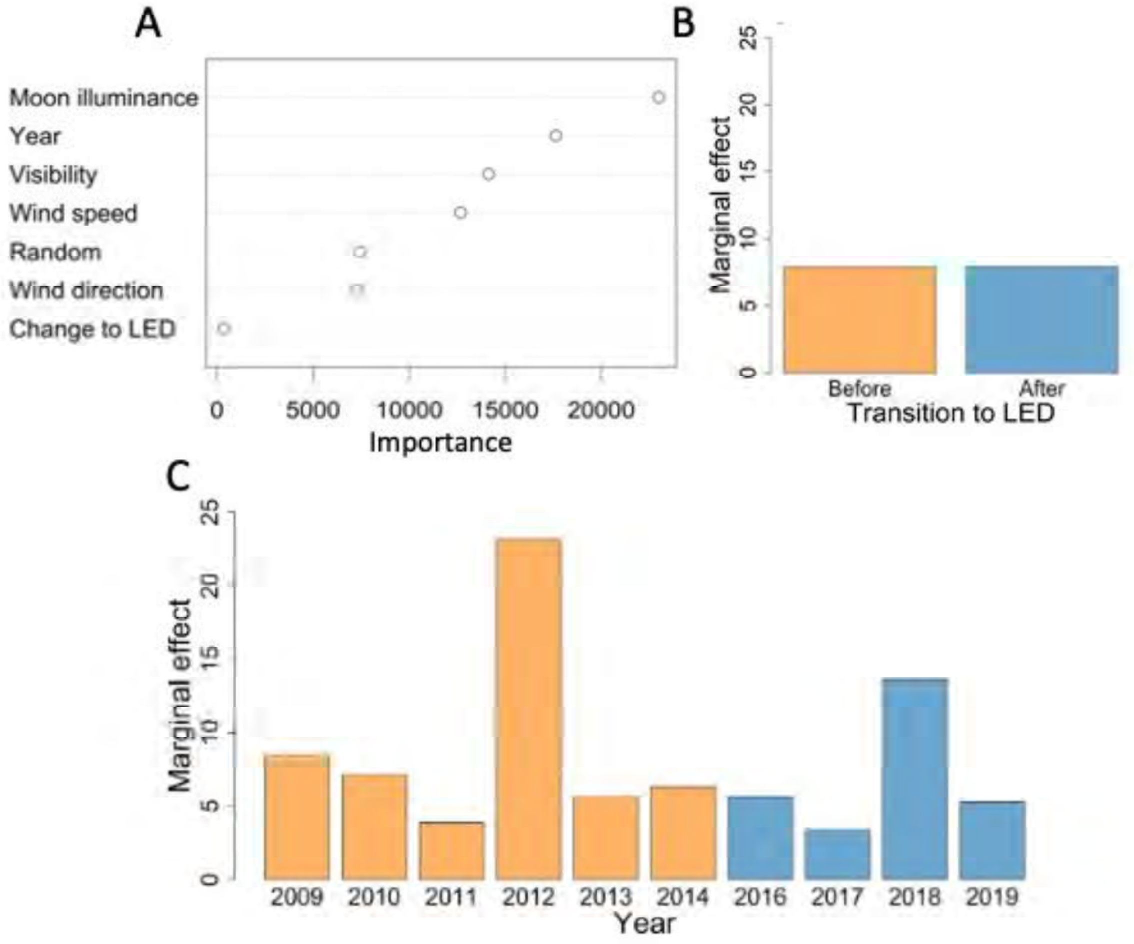

Figure 5.3. (A) Gini index showing relative importance of all parameters. It indicated that moon illuminance and year were the most influential model parameters, followed by visibility, wind speed and wind direction. Change to LED lights contributed less than a random variable to the model. **(B, C)** Partial dependence plots showing a relationship between transition to LED lights (**B**) and years (**C**) on the predicted number of groundings.

DISCUSSION

We show here that a change from sodium to LED lightbulbs in a coastal village close to a major seabird breeding colony was not associated with a decrease in shearwater fallout. We measured light intensity before and after the change in streetlamps and concluded that, overall, the light intensity in Mallaig did decrease in association with the change in bulb type, therefore leading us to predict a decrease in the observed number of grounded birds (Reed, Sincock and Hailman, 1985; Troy, Holmes and Green, 2011; Rodrigues *et al.*, 2012; Glass and Ryan, 2013; Troy *et al.*, 2013). Our model predicting the number of shearwater groundings from environmental variables showed, however, that the transition in lighting was not a good predictor of the number of grounded seabirds, suggesting that switching to LED lightbulbs did not affect shearwater groundings in the village. Similar results have been reported in Hawaii, where a transition to LED lighting did not result in a reduction in the grounding of wedge-tailed shearwaters (*Ardenna pacifica,* Urmston et al., 2020).

A potential reason for this is that as well as light intensity, the spectral composition of the streetlights changed. We do not know how exactly Manx shearwaters perceive different spectra of light (Bowmaker *et al.*, 1997). We may infer, however, that as diving foragers, Manx shearwaters may be more sensitive to blue than red light (Hart 2004). This is supported by observations that higher numbers of birds of closely-related species ground when they are exposed to stronger intensities of the blue part of the light spectrum compared to other parts (Salamolard *et al.*, 2001; Rodríguez, Dann and Chiaradia, 2017), as well as by a stronger behavioural reaction of adult Manx shearwaters exposed to blue lights compared to red (Chapter 2). The bulbs in the village's streetlights mainly changed from warm white low-pressure sodium at 1700 K (Kelvin) and high-pressure sodium at 2700 K to neutral white LED at 4000 K, indicating that the spectrum shifted to blue-rich colours. Thus, the change in light to more disruptive wavelengths may have negated the potential beneficial effect of decreased light intensity which we expected, but failed to observe, in our data. Alternatively, we may not have an accurate measure of change in intensity from the perspective of Manx shearwaters. Light intensity was measured in LUX, which is a unit calibrated specifically to the photosensitivity of the human eye. Thus, even though the light meter recorded a decrease in light intensity for a human eye, this may not reflect perception by Manx shearwaters.

Nevertheless, our model confirmed previous findings that moon and year have a strong influence on the number of grounded birds in Mallaig (Syposz *et al.*, 2018). As in many other Procellariiform species, the presence of a new moon was associated with a greater number of grounded shearwaters (Imber, 1975; Telfer *et al.*, 1987; Le Corre *et al.*, 2002; Rodríguez and Rodríguez, 2009; Miles *et al.*, 2010). Year was the second most important variable, which may reflect exceptional numbers of groundings observed in 2012 and 2018. Unfortunately, there are no yearly data on the breeding success nor on peak fledging of Manx shearwaters from Rum, making it difficult to determine whether these years of high grounding were associated with increased fledgling numbers. While data on average productivity is available for Rum, this did not show statistically significant variations between 1986 and 2018 (JNCC 2020). We speculate, however, that exceptionally successful breeding and changes in the date of peak fledgling may have led to the exceptional grounding numbers in 2012 and 2018. Higher breeding success, as well as date of peak fledgling have been associated with higher fallout in other species of seabirds (Day, Cooper and Telfer, 2003; Rodríguez, Rodríguez and Lucas, 2012; Rodríguez *et al.*, 2014).

Besides moonlight, other environmental variables had an important role in predicting the number of groundings in our model. Both low and high visibility were predicted to be associated with an increase in the numbers of groundings. Adverse weather conditions, like cloudy, rainy nights promote a higher fallout (Phillips and Lee, 1966; Telfer *et al.*, 1987) by increasing light pollution, whereas clear conditions allow light to travel further (Day, Cooper and Telfer, 2003), which may explain this finding. Finally, strong westerly and north-westerly winds were associated with an increase in groundings in our model, likely because strong onshore winds blow flight-inexperienced fledglings in the direction of the light pollution, thus causing higher fallout (Rodríguez *et al.*, 2014). The influence of wind direction, however, was close to that of a random variable, thus we would suggest interpreting this result with caution.

Despite many reports about seabird’s grounding (Rodriguez et al., 2017), it is still unclear why seabirds are found in light polluted areas. The literature suggests that it could either happen due to association between food and light (Imber, 1975; Rodriguez et al., 2017) or incorrect usage of light as a navigation cue (Telfer, Sincock, Byrd, & Reed, 1987). If a seabird associates artificial light with food, we would expect that birds would move towards light pollution showing attraction. On the other hand, if a seabird incorrectly uses light pollution as a navigational cue, we would expect that it would be disoriented. A bird could fly randomly in the vicinity of the light, or move towards the light, or it could circle around it. The low numbers of Manx shearwaters grounded in Mallaig (on average 204 out of a population of 76,000 pairs; Murray, Shewry, Mudge, & Spray, 2003) might suggest that young birds are not attracted towards artificial light pollution of the village directly from the Isle of Rum. It is likely that light pollution only has an effect on Manx shearwaters closer to the village. It is still uncertain, however, if birds are attracted to or disoriented by the light pollution and further studies are necessary to investigate this issue.

CONCLUSION

Our study showed that even though a transition to LED lights in Mallaig resulted in lower light intensity overall, it did not result in a change in the numbers of grounded Manx shearwaters. We suggest that simply lowering light intensity around a village is not sufficient to reduce seabirds' fallout. Thus, we would suggest that future changes to bulbs in places where seabirds ground should consider the perception of seabirds and use LEDs which have more components of red and yellow spectra rather than blue (Salamolard *et al.*, 2001; Hart, 2004; Rodríguez, Dann and Chiaradia, 2017). These higher wavelengths could be additionally beneficial for other species in a range of taxa (Lockley, Brainard and Czeisler, 2003; Evans *et al.*, 2007; Wilson *et al.*, 2018; Fischer, Gangloff and Creed, 2019; Timothy, Samiala and Okrikata, 2019; Williams *et al.*, 2019). Furthermore, measures like shielding of upward radiation, dimming lights, limiting light usage and targeting lamps to avoid skyward spill are likely to further diminish the influence of light pollution on animals (Reed, Sincock and Hailman, 1985; Longcore and Rich, 2004; Miles *et al.*, 2010; Glass and Ryan, 2013; Rodríguez *et al.*, 2014). Governments could balance the safety of humans, energy savings and the reaction of seabirds and other wildlife to implement strategies that are beneficial to all and to support this, studies should be undertaken to observe the impact of lighting changes on wildlife.

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SUPPLEMENTARY MATERIAL

Choosing the weather station

The closest weather station to Mallaig, in Skye, closed in May 2017, thus we had to choose another station to collect our data on cloud cover, visibility, wind direction and speed. The closest weather stations to Mallaig are Tulloch Bridge (70km from Mallaig), Tiree (85km) and South Uist Range (101km, Fig. S5.1). For wind variables (direction and speed) we also extracted forecasted model data from National Oceanic and Atmospheric Administration (NOAA) by using package ‘`rWind`’ (Fernández-López and Schliep, 2019). These data were available only from 2011. We ran correlation tests between the variables collected at each station and the Skye weather station between 2009-2016 and wind variables from Skye weather station and NOAA between 2011-2016 (Table S5.1). Circular correlation (package ‘`circular`’, Lund *et al.*, 2017) tests were conducted to compare wind direction. The variables of cloud cover, visibility and wind direction collected at weather station in South Uist Range were most highlight correlated with those from Skye. Although wind speed data from NOAA was better correlated than those from South Uist Range (0.777 vs 0.664), we chose to take the data from South Uist Range weather station, as all the other variables were better correlated, and it allowed use of a full dataset (2009-2019).

Figure S5.1. Locations of Skye weather station (closed 2017) and three potential alternative weather stations (South Uist Range, Tulloch Bridge and Tiree) for collecting data for the model. Mallaig is pointed with a red dot (OpenStreetMap®, 2020a).

Table S5.1. Results of the correlation test between variables collected at Skye and other weather stations.

VARIABLE	STATION	t	DF	P VALUE	R^2
CLOUD COVER					
	Tulloch Bridge	13.624	940	<0.0001	0.406
	Tiree	12.794	941	<0.0001	0.385
	South Uist Range	15.629	917	<0.0001	0.459
VISIBILITY					
	Tulloch Bridge	7.331	945	<0.0001	0.232
	Tiree	10.553	937	<0.0001	0.326
	South Uist Range	13.438	940	<0.0001	0.401
WIND DIRECTION					
	Tulloch Bridge	10.851	948	<0.0001	0.372
	Tiree	11.227	948	<0.0001	0.398
	South Uist Range	13.996	944	<0.0001	0.52
	rWind	8.436	534	<0.0001	0.397
WIND SPEED					
	Tulloch Bridge	20.695	936	<0.0001	0.56
	Tiree	17.158	945	<0.0001	0.487
	South Uist Range	27.245	942	<0.0001	0.664
	rWind	28.486	532	<0.0001	0.777

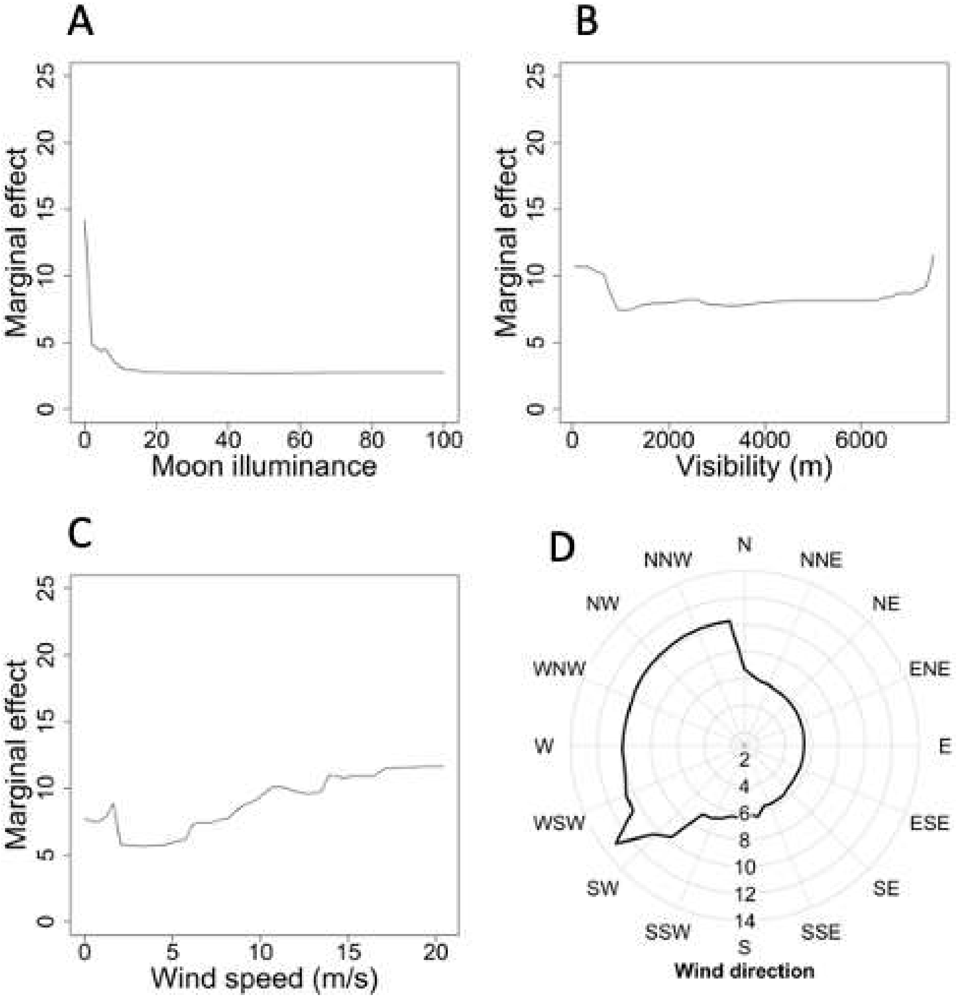

Figure S5.2 Partial dependence plots showing a relationship between a variable (x axis) and predicted number of groundings (y axis). Plots presents the effect of (**A**) the moon illuminance (proxy, arbitrary unit), (**B**) visibility (m), (**C**) wind speed (m/s) and (**D**) direction

A model with a subset of the data

We created a random forest classification model for numbers of grounded Manx shearwaters in harbour area where the systematic survey was undertaken every night. This way we excluded the variability of effort caused by volunteers and public collecting grounded birds. The random forest classification model explained 44.68% variance and showed that the change to LED lights contributed less than a random variable to the model, suggesting that the transition did not have an effect on number of grounded birds in the harbour (Fig. S5.3). The predicted numbers of grounded Manx shearwaters were significantly correlated with the actual numbers ($p < 0.001$, $t = 13.487$, $df = 290$, $R^2 = 0.6209$).

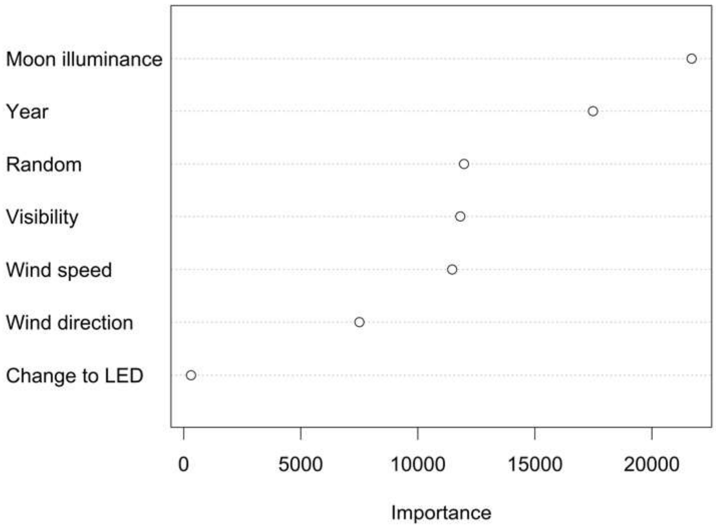

Figure S5.3. The results of random forest classification model for number of grounded Manx shearwaters only in harbour area. Relative parameter importance indicated that change to LED lights contributed less than a random variable to the model.

Chapter 6

General discussion

Introduction

This thesis provides new insights into the influence of light pollution on the orientation of Procellariiform seabirds at different life stages and in various locales. Using novel assays which I have developed for investigating the orientation of Manx shearwaters, both before and during their maiden flights, my results reveal how environmental variables and artificial light pollution interact to affect the maiden flights of shearwaters, adult flight at the colony and, ultimately, drive their grounding.

In this final chapter, I synthesise and link together the key results from this thesis, and present how these findings are informative about broader hypotheses about the link between artificial light at night (ALAN) and the behaviour of seabirds. Additionally, I discuss some of the inherent issues with studying the effects of light pollution on animals, including the limitations of the methods used in this thesis. Throughout this chapter, I propose improvements and avenues for future research into this important field. Finally, I suggest how my findings can aid the conservation of seabirds at their colony and in nearby coastal areas.

Main results and future directions

Throughout this thesis I have investigated different mechanisms by which nocturnal seabirds might be affected by artificial light. In the introduction, I proposed two senses, vision and magnetoreception, that could be disturbed by light leading to significant behavioural changes. Overall, my findings suggest that the behavioural responses of seabirds towards the light are a result of light disturbing a bird's vision rather than their magnetic sense. In the introduction, I also presented primary and secondary response-mediated impacts of light pollution on animals. Within this framework, most of the mechanisms discussed in this thesis should be considered primary responses (i.e. disruption to navigational mechanisms), but, as detailed below, some hypotheses aimed at explaining the results in this thesis could be thought of as a secondary response. Here, I review the evidence from this thesis for magnetic and visual based primary and secondary responses to light pollution in the context of what was known already.

Magnetically mediated light pollution effects

Increasing evidence suggests that light-dependent magnetoreception facilitates the use of the earth's magnetic field for orientation in some species of birds (Wiltschko and Wiltschko, 2005; Mouritsen, 2018). It is now widely believed that, at a molecular level, a 'radical pair mechanism' located in specialised photoreceptors in the eye precipitates a light-dependent, short-lived chemical reaction which modulates a neural signal in response to how the orientation of a bird's head aligns with the geomagnetic field, providing a compass sense (Hein *et al.*, 2010; Hore and Mouritsen, 2016). Very low intensities of full spectrum light are known to be sufficient for the correct functioning of this mechanism (Cochran, Mouritsen and Wikelski, 2004). Studies of captive birds suggest that the wavelengths of light that are critical for orientation are the mid-high energy, green and blue parts of the spectrum (up to 565nm). Conversely, captive birds are disorientated in high intensity red wavelengths (up to 617mm), though they can orientate under lower intensities of red (Wiltschko *et al.*, 1993, 2004; Wiltschko and Wiltschko, 1999; Muheim, Bäckman and Åkesson, 2002).

The reliance of the magnetic compass on a relatively restricted subset of light wavelengths inspires two magnetoreception-related hypotheses for the causes of congregations of birds close to artificial light (Evans *et al.*, 2007; Poot *et al.*, 2008; Guilford *et al.*, 2019; Zhao *et al.*, 2020). Each hypothesis predicts specific wavelength-related effects of ALAN. First, if birds are attracted specifically to light in red wavelengths, this may indicate long-wave light disturbance to the magnetoreceptor, similar to that found in captive bird studies (Cochran and Graber, 1958; Taylor and Anderson, 1971; Avery, Springer and Cassel, 1976; Ogden, 1996; Gautereaux and Belser, 1999). Alternatively, the 'magnetoreception-seeking theory' posits that birds congregate near to ALAN to reactivate light-dependent magnetoreception (Evans *et al.*, 2007). Here, we might expect that high intensities of short wavelength (blue and green) light should have greater attractive properties since they are the wavelengths required for magnetoreception. Unlike the other magnetoreception theories presented here, this mechanism is actually more akin to a secondary (resource seeking or avoiding) response to light (Chapter 1). Due to the low levels of natural light during the night, especially in cloudy, rainy weather, birds may seek brighter areas where their magnetic sense can operate more effectively (Evans *et al.*, 2007). This hypothesis is consistent with some existing observations, principally that bad weather predicts greater numbers of grounded seabirds both at colonies (Guilford *et al.*, 2019) and away from colonies (Telfer *et al.*, 1987). Key therefore to understand (i) whether magnetoreception is involved with seabird ground and (ii) which mechanism is likely to underpin this involvement, is interpretation of the responses of seabirds to different wavelengths of light. Most investigations into the responses of birds to monochromatic light have, however, been limited to passerines. My thesis therefore aims to provide the first in-depth studies of responses to artificial lights of different wavelengths in seabirds.

In Chapter 2, I showed that adult Manx shearwaters which are exposed to artificial light at their breeding colony exhibit an avoidance, rather than attractive, response to the light. This response varied with spectral composition and intensities, which allows for speculation about its influence on the putative magnetic sense of shearwaters. The relevant finding here was that blue and green lights were more disturbing to adult shearwaters than red. No reaction to red light is inconsistent with studies which have found magnetoreceptor disruption in passerines suggesting that the changes in behaviour observed are probably not as a result of flight control at the colony which depends on a radical pair magnetic compass (Muheim, Bäckman and Åkesson, 2002). However, it is possible that during red light treatments, the birds still had sufficient natural light from the stars and moon to permit normal functioning of the light-dependent magnetoreceptor (Cochran, Mouritsen and Wikelski, 2004), masking any effect of the red light itself. This is perhaps indicative of flaws in the theory that birds are attracted to red light because of magnetoreceptor disruption since, in natural free-ranging flight, birds are seldom exposed only to monochrome red light (Cochran and Graber, 1958; Taylor and Anderson, 1971; Avery, Springer and Cassel, 1976; Ogden, 1996; Gautereaux and Belser, 1999). The results presented in Chapter 2 can also be interpreted as evidence against the 'magnetoreception-seeking' hypothesis, since adult shearwaters at the colony were repelled, not attracted, to short-wavelength light despite it being the wavelength most likely to be associated with the radical pair magnetic compass.

In contrast to the results reported in Chapter 2, however, most similar investigations into the responses of birds to light pollution report attraction towards light (mainly passerines, Gautereaux and Belser, 1999; Evans *et al.*, 2007; Zhao *et al.*, 2020), and indeed, Manx shearwater groundings at coastal towns must, on a certain scale, be the result of attraction to lights. There are two key differences that could account for contrasting behaviour of attraction and repulsion reported in Chapter 2. First, the birds are at the colony (not on migration) and second, the birds are not first year birds (all returners to the colony). There is therefore a possibility that Procellariiform seabirds congregate around light-polluted areas only during their migration, when magnetoreception is more important to navigation and so finding places where this mechanism operates effectively is key. Nonetheless, an additional explanation would be required as to why grounding on migration is almost entirely comprised of juvenile birds (Telfer *et al.*, 1987; Le Corre *et al.*, 2002; Rodríguez and Rodríguez, 2009; Miles *et al.*, 2010; Syposz *et al.*, 2018). Therefore, it seems that over the course of shearwater development there is a distinct change in how individuals respond to light pollution. Indeed, developmental changes in navigational mechanisms between first year and adult birds is well known in many species (i.e. the switch from clock and compass navigation to true navigation, Perdeck 1958; Chernetsov et al. 2008).

To summarise, it cannot be ruled out that magnetoreception underpins juvenile responses to light pollution but, since neither experiments in Chapter 3 nor previous studies have found evidence for a magnetoreceptor in seabirds (Massa *et al.*, 1991; Benhamou *et al.*, 2003; Benhamou, Bonadonna and Jouventin, 2003; Bonadonna *et al.*, 2003, 2005; Mouritsen, 2003; Pollonara *et al.*, 2015; Padget *et al.*, 2017), and the wavelengths that shearwaters respond are inconsistent with current magnetic hypotheses (Chapter 2), it seem unlikely overall that magnetoreception is involved with shearwater grounding in response to ALAN.

Further studies in other species which are known to be attracted to light, and that are thought to have a magnetoreceptor could reveal whether this sense could be affected by light pollution. A potential method to test this would be to use a radar to investigate the movement of birds in areas polluted by monochromatic artificial light. Weather surveillance radar data give detailed information about the speed of birds and flock density up to 2km (Van Doren *et al.*, 2017; Becciu *et al.*, 2018; Panuccio *et al.*, 2019), and thus could be an effective means to investigate questions such as (i) how many birds are affected by certain intensities and spectrums of light, (ii) how far the influence of light spreads, and (iii) how movement differs between birds when lights are on versus off. Rapid movements towards light would suggest that birds are attracted to it, whereas slower, undirected changes to bird movement in the presence of artificial light would suggest that they are disoriented by it. Thus, according to current magnetoreception-seeking theory (Evans *et al.*, 2007), we would expect attraction in birds towards blue and green colours. Conversely, if the magnetic sense is disturbed by monochromatic red, then we expect that birds would move randomly when exposed to red colour light. Finally, if, in an area lit by strong blue or green coloured light, birds move randomly, and when red light is turned on, birds do not change their behaviour, it is most likely that their vision, and not magnetic sense, is disturbed by light pollution.

Visually mediated light pollution effects

As with the putative magnetic sense, interference in vision depends upon the spectral composition of the light (Varela, Palacios and Goldsmith, 1993; Muheim, Bäckman and Åkesson, 2002). Unlike in magnetoreception, however, the visual sensitivity of many animal species has been documented in detail, allowing speculation about the impact of light pollution for specific species (Varela, Palacios and Goldsmith, 1993). Furthermore, investigations into the responses of birds towards light pollution possibly reflects variability seen in visual sensitivity – depending on the species used in the study, either long or short wavelengths of lights are reported to be the least disturbing (Varela, Palacios and Goldsmith, 1993; Gautereaux and Belser, 1999; Salamolard *et al.*, 2001; Evans *et al.*, 2007; Zhao *et al.*, 2020). Thus, to ensure that the guidelines for choosing lights minimising animal disturbance are appropriate to the relevant species, a taxon-specific approach has been proposed by some authors (Rodríguez *et al.*, 2017).

In this thesis, I investigated the effect of different spectrums and intensities of light pollution on seabirds from the order Procellariiformes, which allows for speculation about how vision may be disturbed by light pollution. Examination of the spectral sensitivity of one member of this order, the wedge-tailed shearwater (*Ardenna pacifica*), reveals that these seabirds are more sensitive to shorter (blue) than longer (red) wavelengths of light, which has been proposed to be an evolutionary adaptation which facilitates underwater foraging (Hart, 2004). Thus, we can hypothesise that Procellariiformes should react more strongly towards ALAN with blue than red colours. This is supported by a previous study which found smaller numbers of Tropical shearwaters grounding (*Puffinus bailloni*) when red and yellow lights were used compared to green and blue (Salamolard *et al.*, 2001). The results of my thesis are in agreement with these findings and add further insight into the nature of this behaviour and how it varies with life stage. I found that adult Manx shearwaters at the breeding colony avoid blue and green, but not red light (Chapter 2). Furthermore, Chapter 5 showed that a change in streetlights from sodium bulbs to energy-efficient LEDs did not affect the numbers of grounded juvenile Manx shearwaters, even though the light intensity decreased. I propose that this could be due to the associated change in spectral composition, from red and yellow sodium bulbs, to blue-dominant LEDs. Thus, the decrease in light intensity apparent using a human-based measurement (LUX) could have resulted in no change or even resulted in a subjective increase in light intensity from the point of view of the Manx shearwaters. Future research should investigate whether a change from cool (blue rich) to warm (yellow rich) colours of LED bulbs leads to changes in behaviour. If grounding in Procellariiformes is a result of disturbance in vision, a decrease in the fallout would be predicted due to the transition to warm colours, which may be less disturbing for this order.

The varying effects of different wavelengths of light on the behaviour of Procellariiform seabirds (Chapter 2 and 5, Salamolard *et al.*, 2001), as well as a lack of evidence for a magnetic sense (Chapter 3, Bonadonna *et al.*, 2005; Padget *et al.*, 2017), suggest that the grounding of seabirds results from disturbance to vision rather than magnetoreception. As presented in the introduction, there are several ways, fitting in the proposed categories of primary and secondary responses, in which vision may be affected by artificial light. This includes primary influence of light on orientation as result of obstruction of navigational cues (Telfer *et al.*, 1987) or secondary responses to light such as misinterpretation of the light for prey (Imber, 1975; Rodríguez *et al.*, 2017). I proposed that light pollution might also be used erroneously by juveniles as a navigational cue for finding the sea (primary response). Research into sea turtles, species strongly affected by light pollution, reports that hatchlings use light and elevation as cues to help them find the sea (Tuxbury and Salmon, 2005). As water bodies reflect more light than land and vegetation, and the sea is located lower than sand dunes, upon hatching, young sea turtles direct their movement towards the lowest, brightest horizon, which should be a reliable navigational cue (Mrosovsky, 1967; Mrosovsky and Shettleworth, 1968; Limpus, 1971; van Rhijn and van Gorkom, 1983; Salmon *et al.*, 1992; Tuxbury and Salmon, 2005). I proposed that fledging Procellariiform seabirds could also use the brightest horizon as a cue for quickly reaching the sea. I examined this hypothesis in Chapter 4 by designing and creating an arena for testing the orientation of juvenile seabirds on the ground prior to fledging. I found only weak evidence that these seabirds are oriented towards the brightest part of the horizon, which was generally illuminated by light pollution. I concluded, however, that this finding might be due to Manx shearwaters orienting towards the sea using non-visual cues, something for which I also found weak evidence in Chapter 4. I was unable to disentangle environmental variables from the effects of light pollution and the location of the sea on the orientation of fledglings. Thus, it remains unclear whether juvenile seabirds use the luminance of the sea as a cue.

Despite only weak evidence that fledgling Manx shearwaters direct their movement towards the brightest part of the horizon (Chapter 4), I found other similarities between sea turtle hatchlings and seabird fledglings throughout my research, supporting the idea that these groups of animals are affected by light pollution in a similar manner. Chapter 3 revealed that young seabirds fly away from land and towards the sea. Thus, although I found only weak evidence for orientation towards the sea on the ground in Chapter 4, Chapter 3 confirms that when airborne, fledglings do orientate towards the safety of the sea on their maiden flight. It is possible that young seabirds are not able or motivated to orient towards the sea when on the ground - other motivations, such as finding a high place from which to launch or seeking safety from predators, might drive their behaviour instead. Therefore, failing to find an effect here is perhaps not surprising and not inconsistent with the sea being a crucial cue controlling the orientation of birds' first ever flights. Concordantly, after fledging, Manx shearwaters' orientation towards the sea matches the behavioural patterns of newly hatched sea turtles leaving their nest. Therefore, I suggest that further research should be undertaken to investigate the possibility that young seabirds are oriented towards light pollution on their maiden flight. Ideally, this experiment would be undertaken on a Procellariiform colony without ALAN or with artificial light that can be manipulated by a researcher. The vanishing bearings of the departing fledglings could be observed, using the protocols established in Chapter 3. A comparison between the orientations of birds exposed to a light pollution from different compass directions would reveal whether, during their maiden flight, birds use the brightest areas on the horizon as a proxy for the direction of the sea.

Another similarity between shearwaters and turtles is that, like shearwater, sea turtles appear not to be attracted to light pollution as adults. They preferentially select nesting habitats which are away from bright areas (Silva *et al.*, 2017; Hu, Hu and Huang, 2018). Similarly, I found that adult Manx shearwaters avoid artificial light at their breeding colony (Chapter 2). One potential reason for the discrepancy in behaviour between adults and juveniles of burrow-nesting seabirds and sea turtles is that this reflects differences in the developmental stage of the eye (Atchoi, Mitkus and Rodríguez, 2020). Upon fledging, young birds have a well-developed sense of smell but lack the visual sensitivity of adults (Mitkus, Nevitt and Kelber, 2018), thus resulting in the different responses to light between adults and juveniles (Atchoi, Mitkus and Rodríguez, 2020). Such differences in vision have been reported for juvenile and adult sea turtles (Horch *et al.*, 2008). It is, however, unclear whether and how they could be specifically attributed to the differing response towards light pollution in their different life stages. Thus, future research should examine how differences in visual sensitivity in sea turtles may translate into different responses to light exposure, through for example, differences in perception.

To summarise, my findings provide support for the theory that the response of seabirds to light pollution is driven by visual disturbance rather than disruption to the magnetic sense. However, the mechanisms by which this leads juveniles to be affected by light pollution and to ground remain unclear. Similarities in the behaviour of sea turtles and burrow-nesting seabirds suggest that the initial movements of juveniles of both species are driven by motivation to move away from land and towards the sea. Resolving this mechanism is essential to the application of appropriate conservation measures in areas where animals are disturbed by human presence (Salmon, 2006; Deem *et al.*, 2007). It would be beneficial to know if seabirds are oriented towards light pollution during their maiden flight or whether this occurs prior to take-off. It further remains unclear how juvenile seabirds respond to different spectral compositions of light. As my results in Chapter 5 illustrate, clarifying the spectra which drive the misorientation response observed in young birds is essential to minimising their grounding in nearby towns and cities. As the impact of light pollution on wildlife is increasing globally (Kyba *et al.*, 2017), research to determine the point at which behaviour begins to change in response to light pollution, as well as the compositions of light which creates the most disturbance for specific species, is urgently needed.

Limitations

Measuring ALAN

Artificial light can be measured in various ways, including using a digital camera, a sky quality meter, a radiometer or satellite imagery (Muheim, Bäckman and Åkesson, 2002; Prasertkul, 2018; Caruana *et al.*, 2020; Jechow, Kyba and Hölker, 2020; Sanchez de Miguel *et al.*, 2020). While some of these methods measure in detail the spectral composition of light, others give measurements in a unit calibrated specifically to the photosensitivity of the human eye. Throughout this thesis, I used several different methods to describe the spectral composition of artificial light that were appropriate for the specific research but had limitations.

In Chapter 5, I measured light pollution using the human-based unit, LUX, and, using this measure, reported that the transition to LEDs resulted in a decrease in light levels in the village. Thus, I predicted that there should be also a decrease in the observed number of grounded birds. I found, however, no influence of the transition to LEDs on the observed fallout. As LUX does not provide information about the spectral composition of light, I could not speculate about its influence on Manx shearwater groundings. Further investigation revealed, however, that the bulbs in streetlamps were changed from warm white low-pressure sodium at 1700 K (Kelvin) and high-pressure sodium at 2700 K to neutral white LED at 4000 K. Kelvin, usually used as a temperature measure, here indicates a change in spectrum from red to more blue wavelengths. It is therefore possible that while light pollution levels measured in LUX could indicate a decrease in illumination as perceived by human vision, for seabirds sensitive to blue colours (Hart, 2004), the transition to LED light could result in no change or even an increase in light pollution levels. Testing bulbs in a laboratory could reveal the spectral composition of the bulbs used in the village (Muheim, Bäckman and Åkesson, 2002), but for this study was impractical. Different bulbs were used throughout the streets of the village and, beyond the reported measures of Kelvin, further specific details were not recorded about the previously used or new bulbs. Instead, a small, handheld light measure device was used during the fieldwork. Further studies, however, should consider detailed investigations into the spectral composition of bulbs in areas where similar transitions are undertaken.

In Chapter 2, I examined in detail the spectral composition of lights used to determine the responses of adult Manx shearwaters to artificial light, using a spectrometer which recorded in detail the wavelength and absolute measure of intensity of light in luminosity. However, a lack of knowledge of the visual perception of Manx shearwaters precluded a complete understanding of the nature of the behavioural response. Microspectrophotometry has revealed that Manx shearwaters are able to perceive from 402 nm (violet) up until 505 nm (cyan) wavelength light and that visual pigments from the green and red spectrum are present (Bowmaker *et al.* 1997). This is insufficient to determine whether Manx shearwaters in the experiment avoided blue and green light because they perceived higher light intensity or because of the colour itself. To resolve this, further investigations into spectral sensitivity of the visual system of Manx shearwaters would be necessary. However, this only achievable *post-mortem* and therefore requires euthanasia of a healthy animal (e.g. Hart, 2004), raising ethical concerns. Furthermore, whereas from a sensory perspective it is important to understand whether an animal reacts towards specific wavelengths or intensities of light, these details may not be necessary when creating policies regarding light pollution, as effective mitigation could instead be based on behavioural experiments (Deem *et al.*, 2007).

In summary, while ideally the visual perception of a studied animal should be known and considered when undertaking research into the effects of light on behaviour, from a policy-making perspective it may not be essential to understand this in detail, as behavioural responses towards artificial light should be sufficient to create adequate guidelines. When investigating the detailed responses of animals to light, objective measurements of spectral composition, allowing for comparison between species, are the most desirable option when undertaking behavioural tests (Owens and Lewis, 2018). These generic (not animal-based nor anthropocentric) measurements allow for later recalculations that could be useful for both, the creation of legislation relating to light pollution for several species and to create a better understanding of animal behaviour.

Implications for conservation

Growing urbanisation has led to a concentration of environmental problems, such as air, water, plastic and light pollution, as well as biodiversity loss and habitat destruction (Cohen, 2003; McDonnell and MacGregor-Fors, 2016). These ecological risks extend beyond the limits of cities. For example artificial light, if not interrupted by terrain, can extend for considerable distances, influencing animals tens to hundreds of kilometres away from the source (Gaston *et al.*, 2012; Sanchez de Miguel *et al.*, 2020). While some animals have adapted by evolving to avoid light (Altermatt and Ebert, 2016) or conversely by taking advantage of artificially bright areas (Jung and Kalko, 2010; Robertson *et al.*, 2010; González-Bernal *et al.*, 2016), for many other species artificial light poses a serious threat (Speakman, 1991; Stone, Jones and Harris, 2009; Farnworth *et al.*, 2018). Fragmentation of bat habitats, disturbed courtship of glow worms, as well as fatal collisions of many avian species due to light pollution, are all examples of serious conservation concerns caused by ALAN (Kemper, 1964; Stone, Harris and Jones, 2015; Rodríguez *et al.*, 2017; Owens *et al.*, 2020). With rising levels of urbanisation and light usage (Cohen, 2003; Bennie *et al.*, 2015), it is essential to understand how animals will react to light pollution and undertake correct actions against its harmful effects. Recent interest in the effects of ALAN has revealed previously unknown impacts and new species that can be affected (Van Doren *et al.*, 2017; Berge *et al.*, 2020; Cabrera-Cruz *et al.*, 2020; Shier, Bird and Wang, 2020), and this thesis makes new and important contributions to advance our understanding of this field.

The focus of this thesis, burrow-nesting Procellariiform seabirds, are one group of animals particularly negatively affected by light pollution. This group comprises of closely related birds using similar ecological niche and normally active during the day but visiting their nesting sites at night (Warham, 1990). Furthermore, 56 out of 113 species from this group are reported to react to the light pollution in a similar fashion (Rodríguez *et al.*, 2017). Artificial light pollution attracts thousands of seabird fledglings to oil platforms, boats, towns and cities located near to their nesting sites every year (Ryan, 1991; Wiese *et al.*, 2001; Black, 2005; Merkel and Johansen, 2011; Glass and Ryan, 2013; Day *et al.*, 2015; Ronconi, Allard and Taylor, 2015; Rodríguez *et al.*, 2017). Seabirds land on the ground and often are not able to take-off without human intervention. Without rescue, a grounded seabird is vulnerable to predation, dehydration, starvation, poaching or collision with vehicles (Ainley *et al.*, 2001; Rodríguez *et al.*, 2012, 2014, 2017). Estimating the real threat that light pollution poses to seabirds worldwide is difficult as most reports are based on volunteering efforts (Montevecchi, 2006; Rodriguez *et al.*, 2017). Thus, it is likely that the impact on seabird populations is currently underestimated (Ainley *et al.*, 2001). Unfortunately, many affected species are listed as declining, threatened, or endangered, and even a few light-induced fatalities could be detrimental to their populations (Gineste *et al.*, 2017; Rodríguez *et al.*, 2017, 2019). Thus, it is critical to know what actions are necessary to diminish the impact of artificial light on seabirds.

Most of the existing literature surrounding the impacts of light pollution on seabird behaviour has focused on their attraction towards artificial light, as well as the environmental variables influencing their behaviour (Telfer *et al.*, 1987; Le Corre *et al.*, 2002; Miles *et al.*, 2010; Rodríguez, Rodríguez and Lucas, 2012; Rodríguez *et al.*, 2014). However, many questions remain outstanding. For example, it is unknown at what point attraction towards lights starts. Depending on whether birds are orientated towards light prior to take-off, shortly after taking flight, or only when they are already very close to the illuminated area, different guidelines would be appropriate. Thus, understanding in detail how birds are affected by light pollution is crucial when establishing adequate mitigations. This was a key objective of my thesis. Throughout this research I have explored the behaviour of a Procellariiform seabird in response to light and established its varying impact during different stages of life and at different locales. I also examined drivers of grounding behaviour and maiden flight of juvenile Manx shearwaters (Chapter 3 and 5). Thus, my thesis adds to existing knowledge about the set of mitigations required in places where seabirds ground and further stresses the necessity to consider the impacts of light pollution at the breeding colony itself.

In Chapter 4, I aimed to determine at what point birds begin to be affected by light pollution. Previous research, through modelling and analysis of GPS tracks of fledged birds, has explored the effects of light pollution on the maiden flight of fledglings (Troy, Holmes and Green, 2011; Troy *et al.*, 2013; Rodríguez, Rodríguez and Negro, 2015). However, it is not known exactly when in this maiden flight the behaviour of young birds begins to change. I hypothesised that seabirds might already be oriented towards light pollution on the ground at their breeding colony. Chapter 4 provided limited evidence that young Manx shearwaters are oriented towards ALAN at their breeding colony. While this result was restricted to only some of my experimental sites, the risk of juveniles directing their movement towards bright areas when they are already on the ground should be taken into account during fledgling season, as any visible light from a breeding colony could result in increases in the number of grounded birds, compared to when bright areas are only encountered later, during flight. Organisations responsible for sites where breeding colonies are established should take this possibility into account and undertake relevant measures such as light shielding or stopping developments which may be in sight of breeding colonies.

Mitigating the effects of light pollution on seabird behaviour, by lowering light emission, focusing light on targeted areas and changing bulbs is often recommended as a conservation measure (Reed, Sincock and Hailman, 1985; Miles *et al.*, 2010; Glass and Ryan, 2013; Rodríguez *et al.*, 2014; Deppe *et al.*, 2017; Rodríguez, Dann and Chiaradia, 2017). Changing from strobe beam to short light-on pulses, however, has not been previously explored in seabirds. Research in other bird species (mainly passerines) reported that flashing lights are less disturbing than fixed lights, suggesting that birds are able to disperse away from the light and its affect during the dark phase (Tufts, 1928; Baldwin, 1965; Avery, Springer and Cassel, 1976; Wiese *et al.*, 2001; Evans *et al.*, 2007; Gehring, Kerlinger and Manville, 2009). Chapter 2 supports these findings and adds to the literature the first seabird example. Adult Manx shearwaters were less affected by light pollution when they were exposed to shorter, 1-min and 10-min light-on pulses, comparing to 20-minute pulses. Thus, I recommend, whenever possible, the usage of short pulses instead of long ones, for example in radio towers, lighthouses or wind turbines near to seabird colonies. To reduce the duration of time that lights are on in towns and cities, lamps could be turned off periodically or activated via motion sensors.

Changes to the spectral composition of light pollution could also reduce fallout (Salamolard *et al.*, 2001). My findings provide new insights which could refine mitigation measures. In particular, my results in Chapter 2 support emerging evidence that suggests Procellariiformes are more sensitive to blue rather than red and yellow colours (Salamolard *et al.*, 2001; Hart, 2004). Manx shearwaters were observed to exhibit stronger responses to blue and green rather than red light. In conclusion, using bulbs with spectra focused in red and yellow ranges should be recommended in places where seabirds are grounding. While guidelines on changes of wavelength should be taxon-specific (Rodríguez *et al.*, 2017), evidence suggests that long wavelengths are likely to be less disturbing for a range of animals (Longcore *et al.*, 2018).

The impact of light pollution on seabirds varies with environmental variables such as season, weather and moon state, as well as breeding success and peak fledgling date (Imber, 1975; Telfer *et al.*, 1987; Le Corre *et al.*, 2002; Miles *et al.*, 2010; Rodríguez *et al.*, 2014; Syposz *et al.*, 2018). Thus, understanding these effects will help design targeted and effective rescue actions. Conservation campaigns dedicated to rescue grounded seabirds should be encouraged to collect long-term data on colonies and on grounded birds as this will help inform future rescue actions. My analyses in Chapter 5 were possible thanks to long-term efforts to collect data on grounded seabirds. I was able to investigate the effect of transition to LED bulbs in streetlights and define the environmental variables which result in the highest fallout. Using these findings, mitigation measures could be designed to target periods where the risk of grounding is greatest: for example, local communities could be informed when the probability of seabird fallout is highest and encouraged to cover or turn off unnecessary lights (Reed, Sincock and Hailman, 1985; Miles *et al.*, 2010), as well as limit their activities, such as driving (Rodríguez *et al.*, 2012, 2014) and loud parties (Cianchetti-Benedetti *et al.*, 2018).

Efforts to mitigate the effects of light pollution on seabirds should be also undertaken at the breeding colony. In Chapter 2, I reported the first evidence that adult seabirds at the colony might be repelled by light. Literature on the effects of light pollution on birds refers mostly to cases where seabirds are attracted to light (Rodríguez *et al.*, 2017; Van Doren *et al.*, 2017; McLaren *et al.*, 2018; Guilford *et al.*, 2019) and only a few recent publication explore the possibility that birds avoid light (Cianchetti-Benedetti *et al.*, 2018; McLaren *et al.*, 2018; Cabrera-Cruz *et al.*, 2020). Specifically, investigations into the effects of light on seabirds focus mainly around their propensity to ground (Le Corre *et al.*, 2002; Rodríguez, Rodríguez and Negro, 2015; Syposz *et al.*, 2018). Thus, my findings shed new light on seabird behaviour and encourage future research into the effects of artificial light on various species at different stages of life and in different places.

My findings in chapter 2 therefore suggest that avoidance of light pollution by adult seabirds could potentially stop them from approaching the colony. This supports a study of adult Scopoli's shearwaters (*Calonectris diomedae*) which showed that seabirds are repelled from provisioning their chicks due to a loud and bright outdoor event (Cianchetti-Benedetti *et al.*, 2018). Further research is necessary to disentangle the disturbance of high-intensity light and sound. Nevertheless, reports on the impacts of artificial light at the breeding colony suggest that organisations and governments in charge of lighting management, events and buildings should consider their negative effects, and that light should be limited to a minimum near to the colony site throughout the breeding season.

Procellariiform seabirds are the fastest declining group of birds, facing multiple threats, including climate change, bycatch, overfishing, pollutions and invasive and problematic residential species (Croxall *et al.*, 2012; Paleczny *et al.*, 2015; Rodríguez *et al.*, 2019). Many of these risks are hard to address since they require a mitigation of climate change effects, the eradication of millions of rats, or significant changes to fisheries policies (Rodríguez *et al.*, 2019). In contrast, addressing issues of light pollution is relatively straightforward. Here, I have presented recommendations to ensure artificial lighting is minimally disturbing to seabirds, based on the existing literature and new findings from my thesis, and stressed the necessity of their application at relevant times both at the colony and in nearby coastal areas. These actions should consider the effects of the direction, intensity, duration, and spectrum of the lights. Specifically for seabirds, I recommend changing the spectral composition of bulbs to warm colours, a change which may also benefit a range of other animals (Chapter 2 and 5, Longcore *et al.*, 2018). Furthermore, I encourage future research into the impacts of ALAN, particularly given that many potentially harmful effects of light pollution are likely yet to be discovered such as, for example, the unexpected repellent effect of light to breeding adults at the colony (Chapter 2).

Considering that light pollution has been increasing steadily in recent years and is unlikely to decrease in the future, it is essential that mitigation and legalisation is applied in areas which are essential to animals (Kyba *et al.*, 2017; Sanchez de Miguel *et al.*, 2020). The cost of artificial light constitutes as much as ~0.7% of gross domestic product (GDP; Tsao *et al.*, 2010; Kyba *et al.*, 2017). It is possible to reduce both the impact of ALAN on wildlife and the financial costs of artificial lighting by employing recommendations such as decreasing the number of unnecessary light sources, correctly directing lamps to shine only on a targeted area and using motion sensors to reduce the time the light is on (Oliver, 2018). Concerns raised not only by conservation scientists, but also dark sky advocates and the local community, encourages joined efforts to stop the harmful spill of light (Bierman, 2012; Rich and Longcore, 2013; Hecht, 2016; Owens *et al.*, 2020).

Concluding remarks

The work in this thesis focused on understanding the impacts of light pollution on seabirds to help find ways of reducing its negative effects. My findings fill important gaps in our knowledge of the influence of artificial light during different life stages and at various locations. Although these experiments were undertaken on a single species, they are likely applicable to other nocturnal Procellariiform seabirds.

Another key contribution of my thesis is the development of novel, minimally invasive and inexpensive assays to investigate the orientation of birds that could be used on a range of taxa for studying various questions in animal orientation. These will be especially useful for acquiring large sample sizes and for species that are typically difficult to study. I hope my research will inspire further studies into the impacts of artificial light and the specific reasons that birds are affected by light pollution, with the ultimate aim to minimise the negative impact of light pollution of wildlife worldwide.

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