



The effects of temporally distinct light pollution from ships on nocturnal colony attendance in a threatened seabird

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Abstract

The ecological effects from artificial light are complex and can affect species and life-stages differently. Ships are a dynamic source of light pollution, often brightly lit and temporarily increasing light levels in otherwise relatively dark areas. Because several nocturnal seabird species display reduced activity and avoidance of natural or artificial light, we expect that bright vessel lights may affect colony attendance patterns. Here, we test whether the presence of ships in front of coastal cliffs affects colony attendance in the Yelkouan Shearwater (*Puffinus yelkouan*). Ship presence at the site was obtained from an automatic identification system database, and a data logger measured light levels at the colony autonomously for four breeding seasons (2017–2020). Moreover, a Radio Frequency Identification (RFID) system was deployed at a cavernous colony entrance to register arrivals and departures of shearwaters. Direct illumination from ships increased cliff face brightness, and colony attendance was significantly reduced in brighter conditions. Ship presence reduced the number of shearwaters entering the colony per hour by a mean of 18% (SD ± 24). Disruption of natural attendance patterns is likely to have short- and long-term effects on breeding success, physiological condition, and colony viability. Therefore, we propose mitigation measures to reduce the impact from commercial shipping on burrow-nesting seabirds. Local regulations are necessary for colony-specific impact reduction, while incorporation of measures such as black-out blinds, fixture shielding and maximum brightness limits into international conventions can have additional far-reaching benefits.

Keywords RFID · Artificial light · *Puffinus yelkouan*

Zusammenfassung

Die Auswirkungen temporärer Lichtverschmutzung von Schiffen auf die nächtlichen Koloniebesuche einer bedrohten Seevogelart

Die ökologischen Auswirkungen von künstlichem Licht sind komplex und können einzelne Arten und ihre Lebensphasen unterschiedlich beeinflussen. Schiffe stellen eine mobile Quelle von Lichtverschmutzung dar. Häufig hell erleuchtet, erhöhen sie temporär das Helligkeitsniveau in ansonsten relativ dunklen Gegenden. Da diverse nachtaktive Seevogelarten sowohl natürliches als auch künstliches Licht meiden und bei Helligkeit ihre Aktivität reduzieren, ist zu erwarten, dass helle Schiffsbeleuchtungen die Verhaltensmuster von Seevögeln bei ihren Koloniebesuchen verändern können. In der vorliegenden Arbeit testen wir, ob die Anwesenheit von Schiffen vor Steilküsten in Malta die nächtlichen Koloniebesuche von

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Mittelmeer-Sturmtauchern (*Puffinus yelkouan*) beeinflusst. Daten zur Anwesenheit von Schiffen in der Untersuchungsfläche bezogen wir von einer Datenbank des Automatischen Identifikationssystems AIS, während ein Datenlogger über vier Brutzeiten (2017–2020) autonom die Helligkeitsniveaus in der Kolonie ermittelte. Zusätzlich installierten wir ein System zur individuellen Radiofrequenz-Identifikation (RFID) in einem Höhleneingang zur Kolonie, um die An- und Abflüge der Sturmtaucher zu erfassen. Die Beleuchtung von Schiffen führte direkt zu einer erhöhten Helligkeit der Felswand, und die Koloniebesuche waren unter helleren Bedingungen deutlich reduziert. Im Durchschnitt verringerte die Anwesenheit von Schiffen die Anzahl an Sturmtauchern, die pro Stunde in die Kolonie einflogen, um 18% ($\pm 24\%$ Standardabweichung). Vermutlich wirkt sich die Störung der natürlichen Verhaltensmuster in den Koloniebesuchen sowohl kurz- also auch langfristig auf den Bruterfolg, den physiologischen Zustand der Vögel und die Lebensfähigkeit der Kolonie aus. Wir empfehlen daher gezielte Maßnahmen, die die negativen Auswirkungen der kommerziellen Schifffahrt auf höhlenbrütende Seevögel reduzieren könnten. Lokale Vorschriften sind notwendig um den Einfluss auf bestimmte Kolonien zu verringern. Darüber hinaus wäre es von weitreichendem Nutzen, verbindliche Regelungen zu Verdunklungs- und Abschirmvorrichtungen, sowie zu Helligkeitshöchstwerten auf Schiffen in internationalen Konventionen zu verankern

Introduction

Artificial light at night is increasing across the Earth, as are the discoveries of its impacts across multiple taxa (Kyba et al. 2017; Sanders et al. 2021). Some diurnal species extend activity into the night as an effect of higher ambient light, but in contrast, nocturnal species tend to restrict their activity to avoid artificial illumination (Sanders et al. 2021). Several studies demonstrate that even short-term light exposure can cause physiological changes, and while continuous sources of light might attract some organisms, temporary light tends to cause strong aversion responses (Gaston and Holt 2018). The focus of research into light pollution is typically on terrestrial ecosystems, with fewer studies on coastal and ocean habitats (Davies et al. 2014; Gaston et al. 2021). Several artificial light sources affect coasts and oceans including permanent sources such as harbours, coastal urban areas, wind farms and oilrigs, while ships are more dynamic, potentially affecting otherwise dark locations (Gaston et al. 2021). Due to increasing anthropogenic pressure, it is necessary to better understand the effects of artificial light on coastal species and ecosystems (Davies et al. 2014).

Pelagic seabirds in the order Procellariiformes have distinct breeding and foraging areas, often travelling large distances from their terrestrial nests to marine foraging grounds (Oppel et al. 2018). Approximately, 90% of the species in the families Procellariidae, Oceanitidae, and Hydrobatidae, referred to collectively as ‘petrels’, are burrow-nesting and active at colony sites only at night (Keitt et al. 2004; Rodríguez et al. 2019). This behaviour is potentially a foraging optimising strategy (Imber 1975), but also an adaptation to reduce predation risk by diurnal avian predators (Mougeot and Bretagnolle 2000; Riou and Hamer 2008). As a consequence, colony attendance and vocal activity of most petrels are lowered by bright moon light (Watanuki 1986; Keitt et al. 2004), and artificial light from human activities may affect natural behaviour of petrels.

If ambient light levels trigger a response in petrels to reduce predation risk, colony attendance may not only be affected by moonlight, but also by artificial lights (Keitt et al. 2004; Oro et al. 2005; Rodríguez et al. 2015; Cianchetti-Benedetti et al. 2018; Syposz et al. 2021). Light pollution is a recognised threat, which can lead to grounding of fledglings (Le Corre et al. 2002; Rodríguez et al. 2015, 2017b; Crymble et al. 2020b) disorient adult birds (Rodríguez and Rodríguez 2009; Guilford et al. 2018), and attract birds to ships and oil rigs (Black 2005; Ronconi et al. 2015; Ryan et al. 2021). In the Maltese Islands, sub-colonies of shearwaters were abandoned because of development and permanent artificial illumination of cliff faces (Sultana et al. 2011). Moreover, Yelkouan Shearwaters *Puffinus yelkouan* (hereafter referred to as ‘shearwaters’) had higher preference for nest sites sheltered from mainland light pollution (Bourgeois et al. 2008b; Haber 2009). Driven by altered predation risk, European Storm Petrels *Hydrobates pelagicus* have shifted nest preferences away from areas under increasing coastal light pollution (Oro et al. 2005). Despite a preference for darker colonies, there is little information on the changes in petrel behaviour induced by temporary sources of artificial light at breeding colonies. Measurements of any changes in behaviour at colonies can lead to better understanding of expected impacts from increasing artificial light.

One source of temporary light pollution that may affect petrel behaviour is commercial shipping and fishing activity in coastal areas, potentially directly illuminating colony sites (Keitt et al. 2004; Fischer et al. 2021). A specific but common process in commercial shipping is refuelling while at-sea to prevent port congestion, a process termed ‘at-sea bunkering’. Due to the high risk of spills while transferring fuel between ships, adequate illumination of decks and working areas throughout the process is required.

Malta, an island state in the central Mediterranean Sea, is at a strategic position along major shipping routes with several bunkering zones, some of which are immediately offshore of shearwater colonies of international significance.

At these bunkering zones, ships can be present for multiple nights during the shearwater breeding season, thus facilitating a study on the potential impact of temporary light pollution on a seabird colony. To date, there is no information on what effect the industrial shipping activity has on colony attendance patterns of petrels, but a recent study attributes a decline in a penguin population to the noise pollution caused by the establishment of an at-sea bunkering area opposite the colony (Pichegru et al. 2022).

In this study, we determine the effect of higher ambient light, both from the moon and ships, on the number of adult shearwaters entering the colony during the nesting period. We hypothesise that moonlight and the presence of ships increase the brightness of the cliff face, that fewer birds attend the colony when the cliff face is brighter, and that in the presence of ships fewer shearwaters enter the colony. We explore the potential implications of our findings on petrel colonies and recommend management options to reduce industrial light pollution impacts.

Materials and methods

Study area and study species

Yelkouan Shearwaters are typical burrow-nesting seabirds, endemic to the Mediterranean Basin, and currently considered ‘Vulnerable’ to extinction (Dias et al. 2019; BirdLife International 2022). Shearwaters nest in deep, largely inaccessible burrows and caves formed in limestone cliffs. In

Malta, egg-laying typically takes place between late February and mid-March, while incubation lasts around 50 days until late April, and fledging occurs between mid-June and mid-July (Sultana et al. 2011; Gatt et al. 2019).

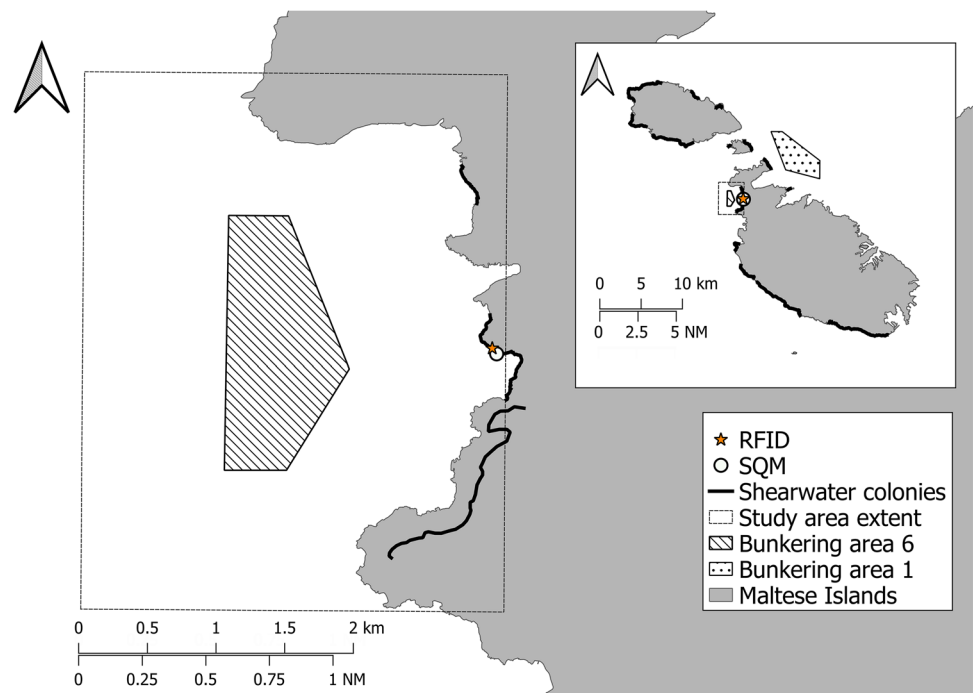
Offshore bunkering in Malta may occur within five designated areas (Transport Malta 2020), two of which (Area 1 and Area 6) are directly offshore of shearwater colonies (Fig. 1). Colonies on the east coast are in direct line of sight of permanent light pollution from coastal towns, but no urban areas directly illuminate the sea cliffs on the north-west coast opposite bunkering Area 6 (Brincat and Pace 2018). Therefore, the effects of light pollution from ships are relevant and measurable.

We conducted our study in a communal breeding cave on the north-west coast of Malta at Majjistral Nature & History Park (MNHP, Latitude 35.95494 N, Longitude 14.33957 E). The single and relatively small entrance to the cave allowed for the set-up of an automated detection system (Radio Frequency Identification, RFID) to measure colony attendance autonomously and continuously. A minimum of 18 to 20 active nests are visible inside the cave, but multiple branches are too deep and too narrow for human access.

Measuring bird activity: RFID system

To quantify the number of birds returning to and departing from the colony every night, we deployed a dual antenna RFID system (Oregon RFID, USA), powered by deep cycle batteries and a solar panel. The two rectangular antennas ($\approx 0.5\text{m}^2$) were placed flat on the ground and approximately

Fig. 1 Map of the study area, including the location of Yelkouan Shearwater colonies (solid bold lines), and the study colony with Radio Frequency Identification system (RFID, filled star) and light meter logger (SQM, unfilled circle). The designated ‘Bunkering Area 6’ opposite the study colony is shown in hashed shading, while the study area extent for which ship presence data was purchased is shown in the dotted rectangle. In the inset map the whole of the Maltese Islands is shown, including ‘Bunkering Area 1’ (dot shading). Distances are shown in nautical miles, in addition to kilometres, because they form the basis of marine regulations, 1 nm = 1852 m



1-m apart, with one antenna further inside the cave than the other, and each spanned the entire width of the cave entrance. A marker tag was placed in between the antennas and used to determine system operation and constant reading range of both antennas. The system was fully operational on 23rd March 2017 and was maintained for the breeding seasons of 2017–2020. The RFID system was in a constant cycle of tag inductive charging pulses (20 ms) and tag reading (30–50 ms), except during the day when shearwaters do not enter or leave the cave.

Adult shearwaters were caught at the entrance of the cave ($n = 132$) or on nests ($n = 4$), and fitted with a metal and a darvic ring on each tarsus. Shearwaters were fitted with 12-mm long glass capsule PITs (Passive Integrated Transponders), attached and covered with marine grade epoxy to alphanumerically coded darvic rings. Each PIT had a unique code which is read by the RFID and associated prior to deployment with each darvic ring.

To classify shearwater movements, we determined a detection of the same individual at the outer antenna (A1) followed by a detection at the inner antenna (A2) as a bird entering the cave ('IN') and vice versa ('OUT'). Typically, multiple in and out movements were made across antennas by individual shearwaters within a night, and therefore we identified arrivals at the colony from the sea as the first 'IN' movement during a night, without having been preceded by an 'OUT' movement on the same night. The final 'OUT' movement during a night, not followed by an 'IN' movement, was identified as the exit from the colony to the sea. All other movements were categorised as cave entrance activity. Our analysis focussed on shearwaters arriving at the colony, while tests on cave entrance activity are provided in the supplementary material. When multiple birds moved over the antennas simultaneously, detection of each individual's tag could be affected. We inspected the last and first detections for each individual on consecutive nights and flagged those detections not made at the same antenna as errors and removed them from all analysis.

Measuring ambient light

To assess whether ships altered the background light levels at the shearwater colony, we installed a light meter data logger (Sky Quality Meter SQM-LU-DL, Unihedron, Canada), henceforth referred to as SQM, pointing towards the cliff face above the cave. While typically used for sky darkness measurements (Davies et al. 2013), SQMs have also been applied to measure the light reflected off the ground (Katz and Levin 2016), or light pollution levels other than at zenith (Kelly et al. 2017). A SQM was used to measure light levels at the cliff face in 10-min intervals and in magnitudes per square arcsecond ($\text{mag}/\text{arcsec}^2$), which we converted to candela per square metre (cd/m^2) following the equation:

$10.8 \times 10^4 \times 10^{(-0.4x)}$ where x is the value in $\text{mag}/\text{arcsec}^2$ (Davies et al. 2013). Cd/m^2 is a more intuitive metric because larger values represent higher brightness.

Ship activity

To relate bird activity and background light levels to the presence of ships, we purchased Ship Automatic Identification System (AIS) data for Area 6 during the periods March to June 2017 and 2018, and for February to June 2019 and 2020 from 'Marine Traffic' (<https://www.marinetraffic.com/>). Data were requested for an extended rectangular area (Latitudes 35.938–35.973 N, Longitudes 14.306–14.340 E; Fig. 1; Fig. S1). The data consisted of ship positions at varying temporal resolution, as part of down sampling algorithms carried out by Marine Traffic. Vessels such as sailing, pleasure and fishing boats were not considered. To obtain the number of ships that were stationary at any one time, records were selected based on a distance change of less than 100 m between successive points for each ship and a reported speed of less than 1.5 knots.

Data analysis

The analysis was carried out in R 3.6.1 and 4.0.5 (R Core Team 2021) run from R Studio v 1.0.143 (RStudio, Inc.). Data and code are publicly available on <https://doi.org/10.5281/zenodo.7003822> (Austad and Oppel 2022).

We first tested whether cliff face brightness is affected by ships in front of the colony. For this purpose, we used only nocturnal SQM measurements (defined as those obtained between the time the sun was 18 degrees below the horizon at dusk on date i and at dawn on date $i + 1$, and calculated for each night using 'sun-methods' in the R package 'maptools' (Bivand and Lewin-Koh 2021). Moonlight intensity was calculated using the package 'oce' (Kelley and Richards 2021), as the product of illuminated lunar disc fraction and moon altitude for the location of our study site. Cloud cover was not included because no fine scale data were available, and cloud cover has a weaker influence on brightness than moonlight. For each 10-min interval between SQM readings, the presence (1) or absence (0), as well as the number of ships was summarised. We then related the SQM-derived light intensity (response variable) to the presence of ships, number of ships and moonlight intensity using a generalised linear mixed model (GLMM) with gamma (log-link) distribution and including the random effects 'hour' nested in 'night', 'month' and 'year' to account for the repeated measures of light intensity. The GLMM and all subsequent models were fit in package 'glmmTMB' (Brooks et al. 2017). Because we expected the influence of ships to vary depending on moonlight, we tested whether an interaction of

moonlight and ship presence significantly affected the SQM-derived light intensity. We concluded that ship presence affected cliff brightness if the parameter estimates for ship presence or the moonlight \times ship presence interaction was significantly different from 0. Moreover, we tested whether the number of ships explained variation in cliff brightness additional to ship presence, by using a likelihood ratio test comparing the full model and a nested reduced model without the variable ‘number of ships’ (Lewis et al. 2011). The number of ships explained additional variation if the two models explained significantly different amounts of variation at $p < 0.05$.

Second, we tested whether cliff face brightness affected the number of individual shearwaters entering the colony. We structured the data into hourly periods between the time when the sun was 6 degrees below the horizon at dusk on date i to the time when the sun was 6 degrees below the horizon at dawn on date $i + 1$. For each hourly interval, we summarised the mean light measurements and the number of individual shearwaters that entered the colony. We then related the number of shearwaters to cliff brightness in a negative binomial GLMM, including the random effects ‘hour’ nested in ‘night’, ‘month’ and ‘year’. To account for temporal variation in shearwater activity, month (factor with five levels for February to June) and time of the night (hourly factor with 12 levels from 17:00 h to 04:00 h UTC) were also included as explanatory variables in the model. We concluded that cliff brightness affected shearwater activity if the parameter estimate for cliff brightness was significantly different from 0.

Our third and most critical question was whether shearwater activity changes when there are ships in front of the colony. We defined a ‘bunkering event’ as nights or consecutive nights with at least two ships present simultaneously and therefore excluded nights when only one ship was present for the entire duration of the night. Bunkering events did not occur in an experimentally controlled fashion, and for this analysis, we retained only those data on bunkering event nights and the two nights immediately before and following bunkering event nights. This approach ensured an appropriate counterfactual measurement of shearwater activity at nights without bunkering ships while controlling for seasonal colony attendance variation (Ferraro and Hanauer 2014). We related the hourly number of shearwaters entering the colony to ship presence, ship number and moonlight in a GLMM with a log-link and a negative binomial error distribution. Moonlight was entered as an interaction term with ship presence. The model included the same temporal variables and random effects as the model from the previous question, with the addition of ‘bunkering event ID’ as a random effect. We concluded that ship bunkering affected shearwater activity if the parameter estimates for bunkering or the moonlight \times bunkering interaction was significantly

different from 0. We predicted the number of birds entering the colony across variable values using the estimated parameters, and then calculated the mean percentage change caused by any effect of ship presence. Finally, we tested whether number of ships explained additional variation by applying a likelihood ratio test comparing the full model and a nested reduced model without the variable ‘number of ships’. The number of ships explained additional variation if the two models explained significantly different amounts of variation at $p < 0.05$.

Results

The RFID system operated for 507 nights within the study period (97% of nights). We recorded 9715 arrivals to the colony by 135 adult shearwaters, of which 1723 were flagged as errors, leaving 7992 for further analysis. Shearwaters entered the colony predominantly in the beginning of the night (Fig. S2). The SQM operated for 472 nights, of which 456 nights overlapped with RFID operation (Fig. S3).

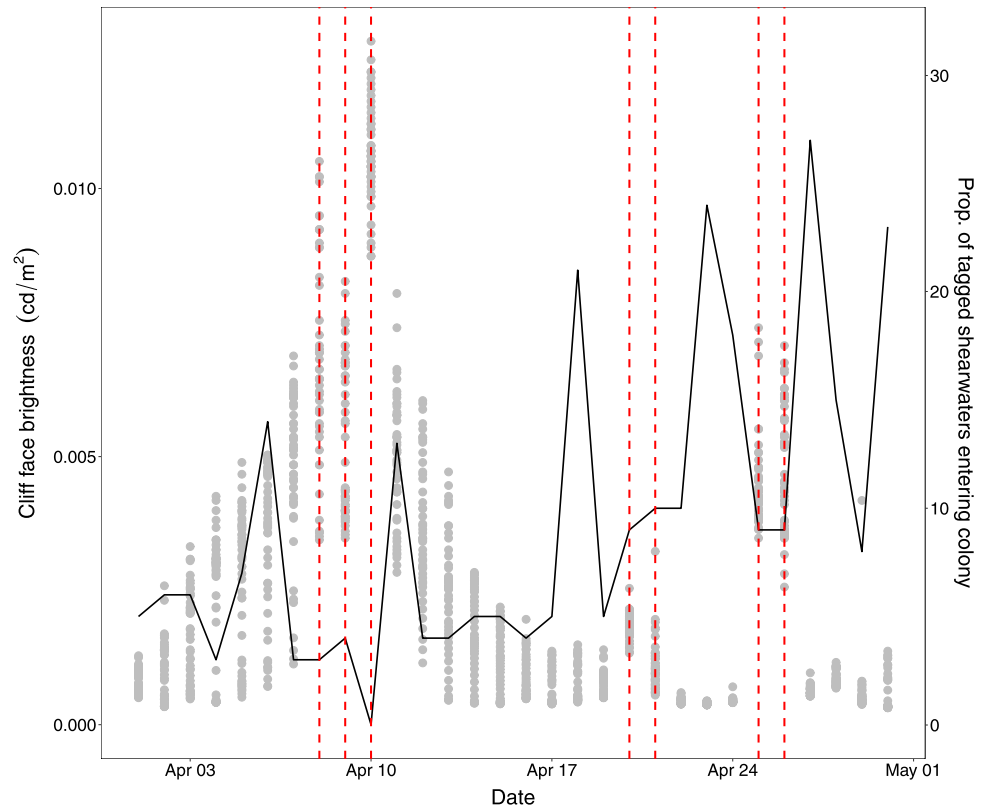
Ships were present in front of the colony on 85 nights (Fig. S4-5; 16% of nights in the study period), while on 14 nights only one ship was present for the duration of the night. We recorded 25 bunkering events, which lasted a maximum of 7 nights (mean = 3 nights $\text{SD} \pm 2$; Fig. S4). Ships were present for a mean of 79% ($\text{SD} \pm 30$) of the night’s duration. During bunkering events, the maximum number of ships present per hour was 14, while the mean was 6 ships ($\text{SD} \pm 3$).

We retained 21,065 nocturnal SQM measurements for the test of the effect of ships on cliff face brightness and found strong evidence for ship presence affecting cliff brightness (estimate = 0.127 ± 0.029 , $p < 0.001$; Table S1; Figs. 2, 3). Cliff face brightness increased with the number of ships present (estimate = 0.112 ± 0.006 , $p < 0.001$), and we found strong evidence that this variable explained additional variation to the presence of ships alone (LR-test $\chi^2 = 298.02$, $p < 0.001$; Fig. 3).

We used 4798 h on 456 nights to test the effect of cliff face brightness on shearwater colony attendance. The number of individual shearwaters entering the colony per hour decreased with higher cliff face brightness (estimate = -12.968 ± 0.984 , $p < 0.001$; Table S2).

To test whether the presence and number of ships affected shearwater colony attendance, we retained 1254 h, on 116 nights with or immediately around bunkering events. The presence of ships, in an interaction with moonlight, reduced the number of shearwaters entering the colony (estimate = -0.295 ± 0.124 $p = 0.017$; Fig. 2; Table S3). In the presence of ships, the number of shearwaters entering per hour was predicted to decrease by a mean of 18% ($\text{SD} \pm 24$) across the range of moonlight conditions. The

Fig. 2 Example period showing the effect of ships on cliff brightness and shearwater movements at Majjistral colony, Malta, in April 2017 (see Fig. S3 for full data series from all four years). Proportion of PIT-tagged Yelkouan Shearwaters entering a breeding cave (solid black line, right Y-axis), as registered by an RFID set-up against cliff face brightness measured with a light meter data logger (grey dots, left Y-axis). The presence of multiple ships, as obtained from AIS data, is presented with vertical lines per night



number of ships did not explain additional variation in colony attendance in comparison with ship presence alone (LR-test, $\chi^2 = 0.343$ $p = 0.558$).

Discussion

Nocturnal colony attendance by a procellariiform seabird decreased in periods when the colony was directly illuminated by ships, in comparison with nights when ships were absent. This is the first time such an effect has been demonstrated for a petrel species in response to a temporary industrial light source with several events of artificial illumination. We obtained these results with an autonomous system, requiring very limited disturbance, and allowing us to demonstrate that presence of ships increases ambient light levels and that colony attendance was significantly reduced in brighter light conditions. Similar light pollution may also affect colony attendance in other petrel species where brightly lit ships operate close to colonies (e.g. Keitt et al. 2004; Guilford et al. 2018; Fischer et al. 2021).

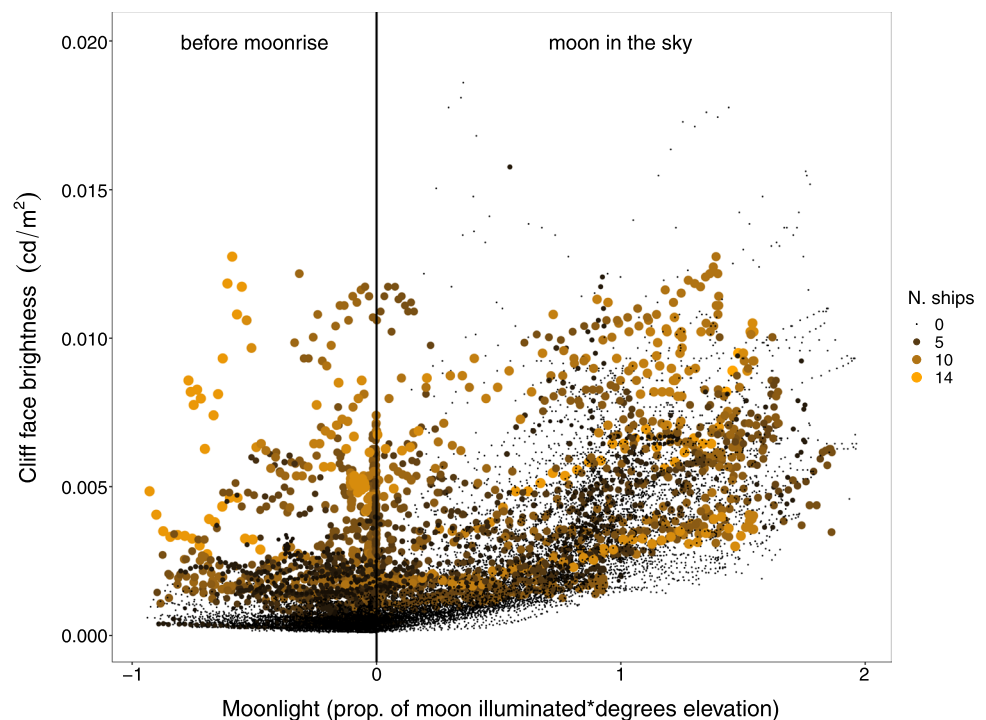
Our results are consistent with the avoidance of light pollution shown in other petrels. In an experimental study, the number of Manx Shearwaters *Puffinus puffinus* in flight around the colony decreased when a bright white light was switched on and the effect was stronger when the light was on for longer (Syposz et al. 2021). Additionally, Scopoli's Shearwater *Calonectris diomedea* chicks in nests

close to an outdoor disco event were fed less than control nestlings (Cianchetti-Benedetti et al. 2018), but the effect of simultaneous light and sound pollution could not be discriminated.

Our study confirms that shearwater colony attendance was affected by ambient light (Table S2), with the brightest ambient light conditions at the colony measured due to the moon alone (Fig. 3). Reduced attendance by adult petrels under strong moonlight has been demonstrated elsewhere, without a lunar effect on cloudy nights when the moon was obscured (Riou and Hamer 2008). Depending on the moon cycle, on most nights petrels can time their arrival to the colony to enter in the darkest period of the night before moonrise or after moonset, with evidence that birds wait for moonset at sea (rafting) near colonies (Keitt et al. 2004; Bourgeois et al. 2008a; Rubolini et al. 2015). However, ship presence at our study colony generally lasted for most of the night and the departure of ships is unlikely to be predictable by shearwaters, leading to the observed reduction in attendance, but may also affect rafting behaviour and energy expenditure. Our results also show that shearwaters typically enter during the first few hours of the night and that the number of colony visits increases during the breeding season, with a peak in May when small chicks require regular feeding.

Adult petrels avoid higher ambient light at colonies to reduce predation risk (Mougeot and Bretagnolle 2000; Syposz et al. 2021). Several diurnal predators of petrels

Fig. 3 Measured cliff face brightness (cd/m^2) at a colony of Yelkouan Shearwaters, Malta, against moonlight, where moonlight is calculated as a function of the proportion of the moon which is illuminated and its elevation in the sky. The solid vertical line marks a moon elevation of 0, the horizon, below which the moon is not visible. The number of ships present at any one time is marked with dot size, size increasing with number of ships present in front of the colony



use moonlight or artificial light to hunt at night, including skuas (Mougeot and Bretagnolle 2000), gulls (Watanuki 1986; Keitt et al. 2004; Oro et al. 2005), and falcons (Rubolini et al. 2015; Miskelly et al. 2022). Yellow-legged Gulls *Larus michahellis* nest in large numbers in the Maltese Islands (Crymble et al. 2020a). The Peregrine Falcon *Falco peregrinus* also breeds on Malta (Sultana et al. 2011), and an individual has been photographed in a shearwater burrow entrance. On Menorca, Peregrine Falcons have captured Balearic Shearwaters *Puffinus mauretanicus* in a cave entrance at night, assisted by moonlight and artificial light pollution from urbanisation (Wynn et al. 2010). An alternative, but not mutually exclusive, hypothesis to the predator avoidance hypothesis, is that moonlight affects foraging efficiency and therefore return rates to the colony (Imber 1975; Mougeot and Bretagnolle 2000). It is unknown whether shearwater foraging is affected by the moon, but they seem to be predominantly diurnal foragers (Péron et al. 2013; Pezzo et al. 2021). Irrespective of nocturnal foraging behaviour, the reduction in return rates we found due to artificial ship illumination of the colony is consistent with the predator avoidance hypothesis.

We were not able to separate between breeders and non-breeders, and we expect that a proportion of tagged shearwaters were prospecting non-breeders. Non-breeders can have a stronger response to ambient light, because they have no parental duties (Watanuki 1986; Mougeot and Bretagnolle 2000). Moreover, non-breeding shearwaters spend more time outside burrows, a behaviour which makes them more prone to predation and more likely to respond to factors that increase predation risk (Bourgeois et al. 2008a). We interpret

the reduced cave entrance activity with higher ambient light and increasing number of ships (Tables S4-S5; Fig. S6) as reduced colony social behaviour especially in non-breeders. In long-lived seabirds with long maturation periods and potentially high site fidelity, the process by which immature birds select colonies is particularly important (Jenouvrier et al. 2008; Votier et al. 2011; Campioni et al. 2017). Moreover, for species suffering from high adult mortality successful recruitment of non-breeders is essential for long-term colony viability (Votier et al. 2008; Oppel et al. 2011). Non-breeders have been shown to visit multiple colonies and recruitment probability increases with colony attendance and conspecific breeding success (Schjørring et al. 1999; Dittmann et al. 2007; Boulinier et al. 2008; Campioni et al. 2017). Therefore, anthropogenic impacts reducing social prospecting behaviour are likely to reduce the chances of recruitment, with long-term implications for colony viability.

Some shearwaters arriving from long foraging trips may enter colonies despite potentially higher predation risk in brighter light conditions, especially to feed chicks (Watanuki 1986; Granadeiro et al. 1998). For example, good condition Manx Shearwater chicks were attended more than poor condition chicks during nights with a bright moon (Riou and Hamer 2008), indicating that there may be individual differences in risk-taking that could affect chick provisioning and fitness (Collins et al. 2019). Whether temporary light pollution by ships ultimately affects chick condition merits further study and is of concern because climate change, food depletion and changes in food web structures also affect chick condition (Quillfeldt et al. 2007; Riou et al. 2011; Rodríguez et al. 2019; Dias et al. 2019; Pezzo et al. 2021). Although

some adult shearwaters attend nests in the presence of light pollution, the physiological impacts are unknown, but may include reduced immune response and increased glucocorticoid stress hormone levels (Ouyang et al. 2017, 2018).

Because breeding petrels avoid anthropogenic light (Oro et al. 2005; Bourgeois et al. 2008b; Syposz et al. 2021) and may collide with ships due to disorientation (Ryan et al. 2021), we advocate against nocturnal ship activity in front of petrel breeding colonies. This is likely to be the most effective conservation measure given that ship presence, and not the number of ships, was more likely to affect colony attendance. In cases where complete banning of night-time shipping in sensitive areas is not possible, we propose several mitigation measures.

1. Reducing the amount of light emitted by each ship, by exclusively using the external lights necessary for safe navigation and operation. Any accommodation lights, especially on ship superstructures, should be blacked out by blinds (Black 2005; Ryan et al. 2021) and light fixtures shielded to avoid light trespass.
2. Using operational light fixtures with a set maximum lumen level sufficient for operational safety, and avoiding short wavelength white light (Syposz et al. 2021), potentially by fitting purpose-designed filters (Rodríguez et al. 2017a).
3. Limiting the number and duration when ships are present in front of colonies, due to the higher potential impact on breeding success from repeated lowered colony attendance.
4. There should be no shipping activity in periods of the breeding cycle when reduced colony attendance by breeding adults will have adverse effects on breeding success. In the case of Malta, this would be the hatching and early chick rearing period in the last week of April and first half of May, which is also when bird activity is highest (Fig. S3).

The International Regulations for Preventing Collisions at Sea (COLREGS 1972) requires revision because of emerging autonomous navigation technology (Zhou et al. 2020), and we advocate that revisions include regulations on ship lighting in ecologically sensitive areas. Moreover, the uptake of mitigation measures would benefit from recognition of artificial light as a pollutant in the International Convention for the Prevention of Pollution from Ships (MARPOL) (Davies et al. 2014). Despite the inclusion of artificial light in the Marine Strategy Framework Directive (MSFD), no measures to establish ‘Good Environmental Status’ have yet been set to ensure efficient monitoring and pressure reduction (Davies et al. 2014; European Commission 2020). Integration of measures aimed at reducing

light pollution from marine sources into international and regional legislation is urgently required.

To conclude, we have demonstrated that despite natural variation in colony attendance, ship presence reduced colony attendance at rates likely to affect breeding success and colony recruitment. Lowered colony attendance shown here in response to temporally distinct light pollution could contribute to colony abandonment caused by permanent sources, advocating against development and outdoor lighting in dark areas. Further study of the effects of light pollution should focus not only on behavioural changes, but also on interaction of light pollution with other stressors and its physiological effects (Ouyang et al. 2018). Finally, we encourage the worldwide ship industry to reduce its environmental impact by taking on board the mitigation measures presented.

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Author contributions MA, PL, BM, SO devised and planned the study; MA, PL, BM, JC, HG, DS conducted the fieldwork; MA, SO conducted the analysis with contributions from all authors; MA drafted the manuscript with contributions from all authors. All authors read the final submitted manuscript.

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Data availability All research was carried out under permits issued by the Environment and Resources Authority (ERA) overseeing protected species and sites in the Maltese Islands. The datasets generated and/or analysed during the current study are available in the Zenodo repository, <https://doi.org/10.5281/zenodo.7003822>.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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