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ORIGINAL ARTICLE

# Understanding the impacts of LED light pollution in marine ecosystems: phototaxis response in fairy prion

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## Abstract

Anthropogenic lighting elicits positive phototaxis responses (i.e. attraction and disorientation) in birds, insects, and many other species across ecosystems. Impacts from lights in marine systems are poorly understood, despite evidence that vessel lighting can cause seabird disorientation and collisions, potentially leading to injury or mortality. The level of attraction/disorientation generated by different types of lighting, including light-emitting diodes (LEDs), is also not well understood in most seabirds. Using fairy prions (*Pachyptila turtur*), a species showing strong positive phototaxis particularly to artificial lights on vessels, we investigated the effects of LED colour and lumen output at a colony during the breeding season. We used six random treatment groups (control = dark, red light, amber low lumen, amber high lumen, white low lumen, and white high lumen) and measured attraction/disorientation responses. Data was analysed using generalised linear mixed-effects models while accounting for environmental variables. Results showed that fairy prions are most impacted by white lights and high lumen output and that a clear gradient exists with increasing attraction/disorientation of birds moving from red to white and at higher levels of brightness. These results agreed with our desktop study, which predicted response rankings based on a related species' spectral response to each light treatment's colour spectrum and lumen output. Furthermore, higher moonlight intensity decreased both abundance and attraction/disorientation responses, and increased cloud cover and more southerly winds were associated with increased abundance, while wind speed decreased and relative humidity increased attraction/disorientation. Our study highlights the need to consider LED colour and lumen output, and environmental conditions in the design of mitigation measures that reduce anthropogenic lighting impacts on land and at sea.

**Keywords** Light pollution · Seabird · Procellariiformes · LED · Vessel · Fairy prion · Anthropogenic light at night

## Zusammenfassung

**Auswirkungen von LED-Lichtverschmutzung in marinen Ökosystemen verstehen: Phototaxis beim Feensturmvogel**

Anthropogene Beleuchtung löst bei Vögeln, Insekten und vielen anderen Arten über verschiedene Ökosysteme hinweg eine positive Phototaxis (d. h. Anziehung und Desorientierung) aus. Die Auswirkungen der Beleuchtung in marinen Systemen sind

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unzureichend erforscht, obwohl es Hinweisen darauf gibt, dass die Schiffsbeleuchtung bei Seevögeln Desorientierung und Kollisionen hervorrufen kann, die zu Verletzungen oder Todesfällen führen können. Der Grad der Anziehung/Desorientierung, der durch verschiedene Beleuchtungsarten, einschließlich Leuchtdioden (LEDs), erzeugt wird, ist bei den meisten Seevögeln ebenfalls ungenügend geklärt. Anhand von Feensturmvögeln (*Pachyptila turtur*) die eine positive Phototaxis insbesondere gegenüber künstlichem Licht auf Schiffen zeigt, untersuchten wir die Auswirkungen von LED-Farben und -Lichtleistung in einer Kolonie während der Brutzeit. Wir wählten sechs zufällige Testgruppen aus (1) Kontrollgruppe = dunkel, (2) rotes Licht, (3) bernsteinfarbendes Licht mit geringer oder 4) hoher Lichtstärke, 5) weißes Licht mit geringer oder 6) hoher Lichtstärke) und maßen die Anziehungs-/Desorientierungsreaktionen. Die Daten wurden mittels verallgemeinerter linearer gemischter Modelle (engl. Generalized Linear Mixed Models) unter der Berücksichtigung von Umweltparametern analysiert. Die Ergebnisse zeigten, dass Feensturmvögel am stärksten von weißem Licht und hoher Lichtleistung beeinflusst werden und dass es einen klaren Gradienten mit zunehmender Anziehung/Desorientierung der Vögel bei einem Übergang von rotem zu weißem Licht und von der niedrigen zur höheren Helligkeitsstufe gibt. Diese Ergebnisse stimmten mit denen unserer Desktop-Studie überein, bei der die Rangfolge der Reaktionsstärke auf der Grundlage der spektralen Reaktion einer verwandten Art auf das Farbspektrum und die Lichtleistung der einzelnen im späteren Versuch verwendeten Lichtbehandlungen vorhergesagt wurde. Weiterhin verringerte eine höhere Mondlichtintensität sowohl die Abundanz als auch die Anziehungs-/Desorientierungsreaktionen. Stärkere Bewölkung und südlichere Winde wurden mit einer erhöhten Abundanz in Verbindung gebracht, während die Windgeschwindigkeit die Anziehung/Desorientierung verringerte und die relative Luftfeuchtigkeit diese erhöhte. Unsere Studie betont die Notwendigkeit, LED-Farbe und -Lichtleistung sowie die Umweltbedingungen bei der Entwicklung von Maßnahmen zur Verringerung von anthropogenen Beleuchtungsauswirkungen an Land und auf See zu berücksichtigen.

## Introduction

It is well known that anthropogenic light at night (ALAN) acts as a beacon that attracts many species, including birds, insects, and other taxonomic groups. Many bird species are attracted to lights, which can cause disorientation, groundings, and collisions with structures (Holmes 2017). For the purposes of this study, we defined attraction as birds flying towards the light source and disorientation as birds deviating from a straight path, which is referred to herein as a single combined attraction/disorientation response. The impacts of lighting attraction on strandings for various seabird species have been well documented (Cieraad and Farnworth 2023; DCCEEW 2023; Heswall et al. 2023). A recent study by Brown et al. (2024) suggested alternative hypotheses to light attraction should also be explored. Differences in species phenotypes can result from ontogenetic development (Atchoi et al. 2023; Brown et al. 2023, 2024) as well as interspecific variation between flying and flightless seabirds (Rodríguez et al. 2018). Although diurnal species are also affected, nocturnal species are particularly sensitive to the disruption of natural darkness by artificial light. Nocturnality in many species, including seabirds, is believed to be a trait that developed as a defence mechanism against predation (McNeil et al. 1993; Mougeot and Bretagnolle 2000) and evolved independently of the artificial lighting pressures that are now persistent in natural environments. This adaptive behaviour is commonly referred to as a predator avoidance response.

The impacts of light at night are determined by species' physiological and ecological traits, combined with the characteristics of light emissions (including colour, intensity, and timing). Spectral sensitivity is species-specific (Mitkus et al. 2016; Syposz et al. 2021; Longcore 2023). Generally, seabirds respond more to blue, violet, and ultraviolet wavelengths and less so to warmer colours like amber or red wavelengths (Campos 2017). Most petrels (Procellariiformes), including fairy prions (Tītī wainui, *Pachyptila turtur*), are nocturnally active at colonies. They differ from other seabird species in that they are predominantly adapted to flying at night during colony attendance (Mougeot and Bretagnolle 2000; Rodríguez et al. 2019). However, the current body of evidence is divided. For example, some Procellariiformes are attracted to light (e.g. fairy prions), whilst others (e.g. Manx shearwaters *Puffinus puffinus*) are both attracted and repelled with research findings highlighting that factors such as environmental conditions, age class and ontogeny play a role in light attraction for seabirds (Guilford et al. 2019; Atchoi et al. 2020; Syposz et al. 2021).

Most studies determining lighting impacts at night have been land-based (Rodríguez et al. 2017b); however, impacts can also occur at sea. For example, lighting from marine vessels or oil platforms can result in unintended consequences such as seabirds flocking towards the light source (positive phototaxis) and subsequently colliding with illuminated structures (Ronconi et al. 2015; Ryan et al. 2021). Known as deck or vessel strikes, it is a widespread phenomenon internationally and of growing conservation concern (Rodríguez et al. 2017b; Coleman et al. 2022). Marine vessels differ in the types of lighting used. The health and safety of staff and the need to perform various tasks at night (e.g. deployment and recovery of fishing gear and/or cleaning of decks) are the primary considerations in the selection and use of vessel-mounted lights for fishing vessels (pers. comms. D.G). In New Zealand, the Department of Conservation (DOC) has played a key role in raising awareness within the New Zealand fishing and cruise ship industries of the need to reduce lighting impacts. Mitigation Standards (DOC and MPI 2023) include eliminating non-essential operational lights, minimising and shielding all other lighting (e.g. using window shading), and avoiding high-risk areas to seabirds such as breeding colonies.

Technological advances, such as the availability of energy-efficient LED light sources in many colours and lumen outputs, provide opportunities to tailor outdoor environmental lighting requirements. However, while there are measures in place to help reduce at-sea light attraction to seabirds, little research has focused on how LED colour and the amount of light being emitted can be used in vessel-related mitigation strategies (Rodríguez et al. 2017a). Our study aims to address that knowledge shortfall, focussing on fairy prions, a species with a history of attraction to, and interaction with, fishing and cruise ship vessels at night, including in the Marlborough Sounds (Te Tau Ihu o Te Waka-a-Maui), New Zealand (Aotearoa) (pers. comms. J.F.). Specifically, we investigated the effects of LED colour and lumen output on the abundance and behaviour of adult fairy prions at a colony during the breeding season using an experimental setup with six different light treatments, while accounting for environmental conditions. We expected to see decreased responses associated with lower colour temperatures and lower lumen outputs. We also conducted a desktop study to predict response rankings based on each light treatment's colour spectrum and lumen outputs, and a related species' spectral response.

## Materials and methods

### Study location and timing

Light exposure experiments were undertaken on Stephen's Island (Takapourewa), an uninhabited remote island at the north of the Marlborough Sounds, Cook Strait, New Zealand (latitude −40.6693817, longitude 173.9999533). Stephen's Island has a land area of 1.5 km$^2$ and rises 283 m above sea level. Trials were conducted along the eastern side of the island at an altitude of 173 m above sea level (Fig. 1). An active lighthouse and sporadically occupied staff cottages are located at the northern end of the island, about 1 km away from the study site. However, no lit structures can be seen from the study area. Stephen's Island is exposed to vessel traffic passing en route to, and beyond, Cook Strait and Tasman Bay (Te Tai-o-Aorere). The study took place over 17 non-consecutive nights during the period from 8th December 2022 to 18th January 2023.

### Study species

Adult fairy prions (Procellariidae, Fig. 2b) were chosen as the study subjects as they are known to be attracted to vessel lights (pers. comms. J.F.). They are among New Zealand's most abundant and smallest petrels, weighing up to 160 g. Protected under the New Zealand Wildlife Act (1953), they breed in large numbers, predominantly at colonies south of Cook Strait (Te Moana-o-Raukawa) to the sub-Antarctic islands. The largest population of fairy prions is on Stephen's Island where colony numbers are in excess of one million breeding pairs (Taylor 2000). Spending most of the year at sea, they return to small offshore islands to breed in caves or burrows. They do so from dusk under the cover of darkness with the majority having returned by around midnight in December and January (pers. obs. K.M). The breeding season is typically from October to February, with egg laying taking place in November. Experiments in the current study were conducted from December to January before fledging when most breeders were rearing chicks. Adults and juveniles are known to exhibit different reaction times to light emissions (Rodríguez et al. 2017b; Atchoi et al. 2024); therefore, the population was monitored to ensure fledglings were not included in the dataset.

### Equipment

#### Lighting rig

A lighting rig was fitted with red, amber, and white light sources for the experiment (Fig. 2c). Red light was provided by six 24 V DC Bee Calm LED luminaires. Each was rated at 800 lumens, providing a total of 4,800 lumens for this treatment. Marine-grade long-range HELLA HypaLUME LED luminaires with twin light bars were used to provide 2500 K amber and 5700 K white light (1GJ 958 334–121 and 1GJ 011 872–511, respectively). The amber light at full power was rated at 19,000 lumens and powered with 24 V DC ("amber high"), and the white at full power with 240 V AC was rated at 28,000 lumens ("white high"). A shade was used to cover one of the amber light bars to provide a half-setting (amber low). The white low setting was provided by switching off one of the white light bars. Lights were chosen based on current use in New Zealand commercial fisheries. Please note that lumens are used describe luminaires in this experiment, as this is standard in lighting specifications. However, this photometric unit is based on the spectral sensitivity function for the human photopic eye. The methods used to convert from human-based metrics to a seabird's visual system are discussed in the Spectral response section below.

All lights were powered by a Honda eu20i petrol generator, which ran continually throughout all experimental and

**Fig. 1** Stephen's Island, New Zealand, study location and position of the lighting rig. Inset map sourced from Land Information New Zealand (Crown Copyright Reserved). Island image sourced from Google Earth

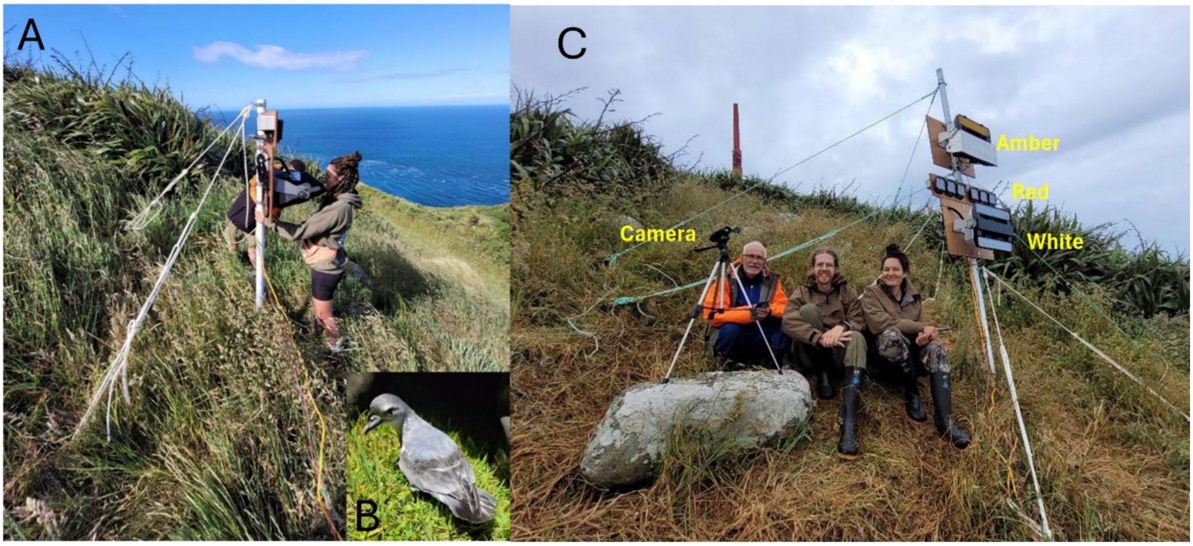

**Fig. 2** Aspect of the lighting rig showing the slope of the island (**A**), fairy prion study species (**B**), and position of the thermal imaging camera relative to the lighting rig with amber, red, and white lights (**C**). Photo credit: K.L. Middlemiss

control periods. The noise level was equal across all treatments and was not accounted for in the statistical model, as the lighting rig could not be operated without running the generator. The lights were attached to a vertical pole and positioned parallel to the sea surface (Fig. 2a,c). The lighting rig was positioned facing seawards, to the southeast, and the ground sloped downwards towards the sea at an approx. 50° angle.

### Thermal imaging camera

Video footage was gathered using a Pulsar Helion XP38 thermal imaging camera which enabled data extraction on abundance, and attraction/disorientation (Fig. 2c) (objective lens: F38/1.2, field of view:11.4° horizontal × 8.6° vertical).

## Experimental design

Each experimental night started at 22:00 h to align with dusk at around 21:00 h and the onset of fairy prions returning to the colony under the cover of darkness. In total, 17 non-consecutive nights were sampled, spanning 1.5 lunar cycles (electronic supplementary material Fig. S1). Each experimental night comprised three blocks and each block consisted of a randomly assigned order of all six light treatments (light on for 1 min in each treatment), which were each separated by a 5-min dark interval (light off). Treatments included a control ("dark", no anthropogenic light), red light, high and low lumen amber light, and a high and low lumen white light. Each block lasted 31 min (6 × 1 min light treatment, with 5-min interval separating each treatment), and the three blocks were also separated with a 5-min interval without treatment. In addition to recording bird abundance and behaviour using the thermal camera, we also used individual paper recording sheets each night to annotate the number of grounded birds, collisions with the lighting rig, and data on environmental covariates.

## Environmental data

Environmental data was sourced from the Meteorological Service of New Zealand weather station located at the northern end of Stephen's Island (latitude −40.664926, longitude 174.000271), approximately 1 km from the study site. Variables of interest included wind speed, wind direction, relative humidity, and precipitation (no precipitation occurred on any of the 17 nights). Wind speed and direction were separately included. For wind direction, the extents of eastward and northward winds were calculated as the sine and cosine of the wind direction, respectively. In addition, local on-the-night data was recorded during the experiment nights at the beginning and end of each treatment, including the percentage of cloud cover and whether the moon was visible in the sky or obscured by surrounding hills or clouds. We calculated moonlight intensity, i.e. lunar illumination received on the ground (rather than moon phase or proportion of the moon disc illuminated), as this is a good predictor of animal activity, using the *moonlit* package in R (Śmielak 2023).

## Video review

Consecutive video clips were stitched together for each night's footage, without rendering, using open-source *Avidemux* software, and reviewed by one researcher. Clips of each treatment minute and the dark period 1 min before each treatment were reviewed twice to establish bird abundance, and bird attraction and disorientation (referred to collectively as attraction/disorientation) separately. To estimate bird abundance, the footage was reviewed at two-thirds speed, and the number of birds visible in the frame was counted at 10, 20, 30, 40, and 50 s into each treatment. The second review was conducted at half speed to count the combined number of instances that birds flew towards the camera/light (which we assumed to represent attraction to the light, i.e. a proxy for positive phototaxis) over the whole minute and those birds that deviated (i.e. any angle) from a straight path and turned towards the centre of the light beam (which we assumed to represent birds that were confused, disoriented, and/or trapped by the light). Birds could not be individually identified, so it is possible that some individuals may have been counted more than once, although the authors feel this is likely to have been minimal given the short 1-min sampling period. The resulting behavioural response variable consists of the total number of instances of attracted/disoriented birds, as the two types of responses could not be distinguished, or individual birds identified.

## Spectral response

Following the approach of Aubé et al. (2013) and Longcore et al. (2018), we computed the spectral response index (SRI) for each light treatment. This index represents the degree of overlap of our light sources' spectral power distribution (SPD) curves with a species' spectral response curve, with reference to the D65 standard illuminant for daylight from the International Commission on Illumination (CIE). The SPDs were obtained for the amber and white light from the manufacturer, and the red lamp was tested by the lighting laboratory at Massey University. The wavelengths ranged from 380 to 750 nm to match the outer limits of the light sources' response. The SPD curves were resampled to 5 nm increments to ensure consistency for all light treatments. The curves were then normalised for a constant lumen output using the CIE photopic spectral sensitivity function $V(\lambda)$ (Longcore et al. 2018). This normalisation was chosen to ensure that the light sources provided equal visual stimulus to humans, as the primary purpose of electric light on marine vessels is to illuminate human activity. The normalisation method to find $\Phi_{n(\text{lamp})}(\lambda)$ is given in Eq. 1, where $K_m$ is the maximum value of the spectral luminous efficacy ($\approx 683\ \text{lm}\bullet\text{W}^{-1}$), a mathematical constant that is needed to convert data to lumens (CIE 2014).

$$\Phi_n(\lambda) = \frac{\Phi(\lambda)}{K_m \bullet \int_{380\text{nm}}^{750\text{nm}} \Phi(\lambda) \bullet V(\lambda) \bullet \mathrm{d}\lambda}. \tag{1}$$

SPD curves for the light treatments are shown in Fig. 3, together with other relevant curves that will be discussed in the following paragraphs.

Due to a lack of published research on vision in fairy prion and/or close relatives, we used the spectral response curve for Bonin petrel (*Pterodroma hypoleuca*) from Longcore (2023), original data from Reed (1986). Bonin petrels have a similar ecology to fairy prions, with birds of both species returning to their colonies at night during the breeding season, which we expect results in a similar eyesight adaptation for low-light conditions. We normalised the spectral response curve to one at its maximal value and annotated this as $S(\lambda)$ (refer to Fig. 3).

As noted above, we chose to reference all calculations to the standard SPD for daylight, which is the CIE D65 standard illuminant. Using Eq. 1, the D65 SPD was normalised to provide $\Phi_{n(D65)}(\lambda)$. To find the SRI we first computed the lamp SPD as weighted by the spectral response curve. We then used the same methodology to calculate the weighted D65 SPD. The ratio of the weighted lamp SPD over the weighted D65 SPD was then used to provide the SRI, per Eq. 2.

$$\text{Spectral response index} = \frac{\int_{380\text{nm}}^{750\text{nm}} \Phi_{n(\text{lamp})}(\lambda) \bullet S(\lambda) \bullet d\lambda}{\int_{380\text{nm}}^{750\text{nm}} \Phi_{n(D65)}(\lambda) \bullet S(\lambda) \bullet d\lambda}. \tag{2}$$

As the SRI is normalised for constant lumen output, the impact of a particular treatment can be found by multiplying the SRI by the light output in lumens. This allows us to scale the results and determine the combined effects of the different light treatments' spectrum and intensity.

## Statistical analysis

Statistical analysis was carried out in R version 4.4.0 (RTeam 2024). To evaluate differences in the number of birds observed between treatments, generalised linear mixed-effects models were used within the *glmmTMB* package (Brooks et al. 2017). The response variables were bird abundance (the number of birds observed in the field of view, repeated five times within each treatment period) and the number of attracted/disoriented birds. Abundance counts were fitted with a Poisson distribution, while attracted/disoriented counts were fitted with a negative binomial distribution to account for overdispersion. To account for a variation in bird counts through the night (Fig. S2, S3), we could have used counts from the dark 'control'; however, as activity can change rapidly over time and with treatments being up to 1 h apart, we instead used bird activity in the dark period immediately prior to the treatment. We incorporated an offset of the count during a 1-min dark period immediately prior to the treatment by adding an offset model term. The mean number of birds counted at each 10-s interval, and the number of attracted/disorientated birds over the 1-min previous

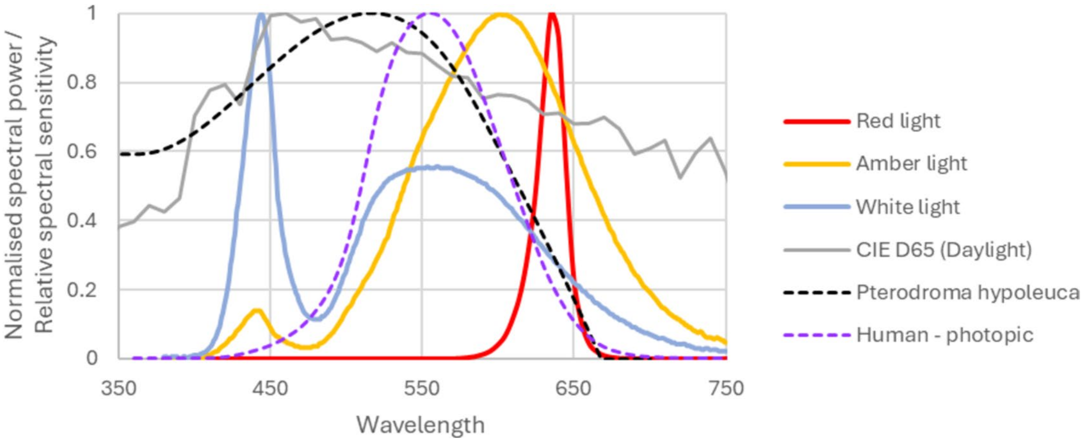

**Fig. 3** Normalised spectral power distributions for the three treatment light sources and CIE D65 daylight are indicated by solid lines, and dashed lines represent relative spectral response curves of *Pterodromo hypoleuca* (as a proxy for fairy prion, S(λ)) and human photopic vision (V(λ))

dark period, was used as the offset for the abundance and attracted/disoriented responses, respectively. In both cases, if this count was zero, a count of one was used.

A random effect of treatment blocks nested within nights was included to account for differences in the number of birds between nights and segments of each night. For the abundance measure, multiple measurements (5- × 10-s interval counts, 'time into treatment') per treatment were accounted for by adding treatment to this nested random effect. Fixed effects included treatment (five treatment light colours and a dark control), as well as relative humidity, cloud cover, wind speed, eastward and northward wind direction, time after sunset, and the interaction between moon visibility and moonlight intensity. For the abundance measure, we also included the time into treatment as a fixed effect. For each response variable, a full model that included all fixed effects, offset and random effects was constructed. We assessed all constituent models using the dredge function in the *MuMIn* package (Barton 2023), and the top-ranking models were selected using the corrected Akaike information criterion ($\Delta \text{AICc} \leq 2$).

The *DHARMa* package (Hartig 2023) was used to check model diagnostics, including distribution assumptions, heteroscedasticity, and outliers. The top-ranking abundance model had a slight pattern in the second and third quantile residuals, while in the top-ranking attraction/disorientation model there was a significant hump shape in the residuals, which was not related to any of the predictor variables; this patterning could not be fully alleviated with various model forms. Post hoc differences between treatments and confidence intervals were assessed using the *emmeans* package (Lenth 2023).

## Results

### Bird abundance and behaviour (attraction/disorientation) counts

Bird abundance showed considerable variation between treatments. Typically, fewer than 20 individuals were counted in the video frame during any 10-s period. Results of the top-ranking model showed significant differences between some treatments ($p < 0.001$), with the control treatment having significantly fewer birds than the high lumen amber treatment, and low and high lumen white light treatments (Fig. 4a; Table 1). Counts increased as time progressed into the 1-min treatment period (time in treatment) and with increasing cloud cover; and counts decreased with wind from a more northerly direction, and brighter moon illumination (Table 1). Models that included additional predictors of wind speed, easterly wind, and time since sunset also gained substantial support ($\Delta \text{AICc} \leq 2$; electronic supplementary material Table 1).

Counts of birds flying towards the camera/light and those turning within the frame during the 1-min treatment were used as a proxy for birds attracted/disoriented by the light. Clear differences in the numbers of individuals exhibiting attraction/disorientation behaviours between light treatments (Fig. 4b). The number of birds displaying these behaviours did not significantly differ between the dark control and red light, whereas all other treatments resulted in significantly more attracted/disoriented birds ($p < 0.05$). In general, treatments with a higher lumen output and whiter light resulted in higher counts (Fig. 4b). Lower moonlight intensity, higher humidity, and lower wind speeds were associated with an increase in attracted/disorientated birds (Table 1) in the most parsimonious model of the 11 top-ranking models ($\Delta \text{AICc} \leq 2$), while the top model also included the (non-significant) effects of cloud cover and time since sunset. Other top-ranking models ($\Delta \text{AICc} \leq 2$) also showed some support for moon visibility and wind direction (electronic supplementary material Table S1).

Across experimental nights, seven low-speed collisions occurred with the lighting rig: one during a red treatment, three during amber low treatments, one during an amber high treatment, and two during a white low treatment. A total of 34 birds were grounded during treatments with higher numbers in treatments with higher lumen output and whiter light (Fig. 5). No birds were harmed, and all were retrieved and released immediately.

### Desktop-based study of spectral sensitivity

Using the Bonin petrel as a proxy spectral response curve, amber light is predicted to have the least effect per lumen (0.562), followed by red (0.667) and white light (0.808) (Table 2). As the experimental lamp treatments have different intensities, it is vital to include the effects of lumen output rather than considering spectrum alone. Column 4 of Table 2 predicts the combined effect of spectrum and lumen output and shows that the 4,800-lm red light has the least impact. At the other extreme, the 28,000-lm white high treatment is predicted to have over seven times the effect of red light. Falling between these two figures, the amber low treatment has nearly double the impact of red, while amber high and white low have similar responses of 10,678 and 11,312, respectively. The ranking of the predicted spectral response indices for the rated output of our treatments conformed with the observed ranking of the impact of the treatments (cf. Figure 4, Table 2).

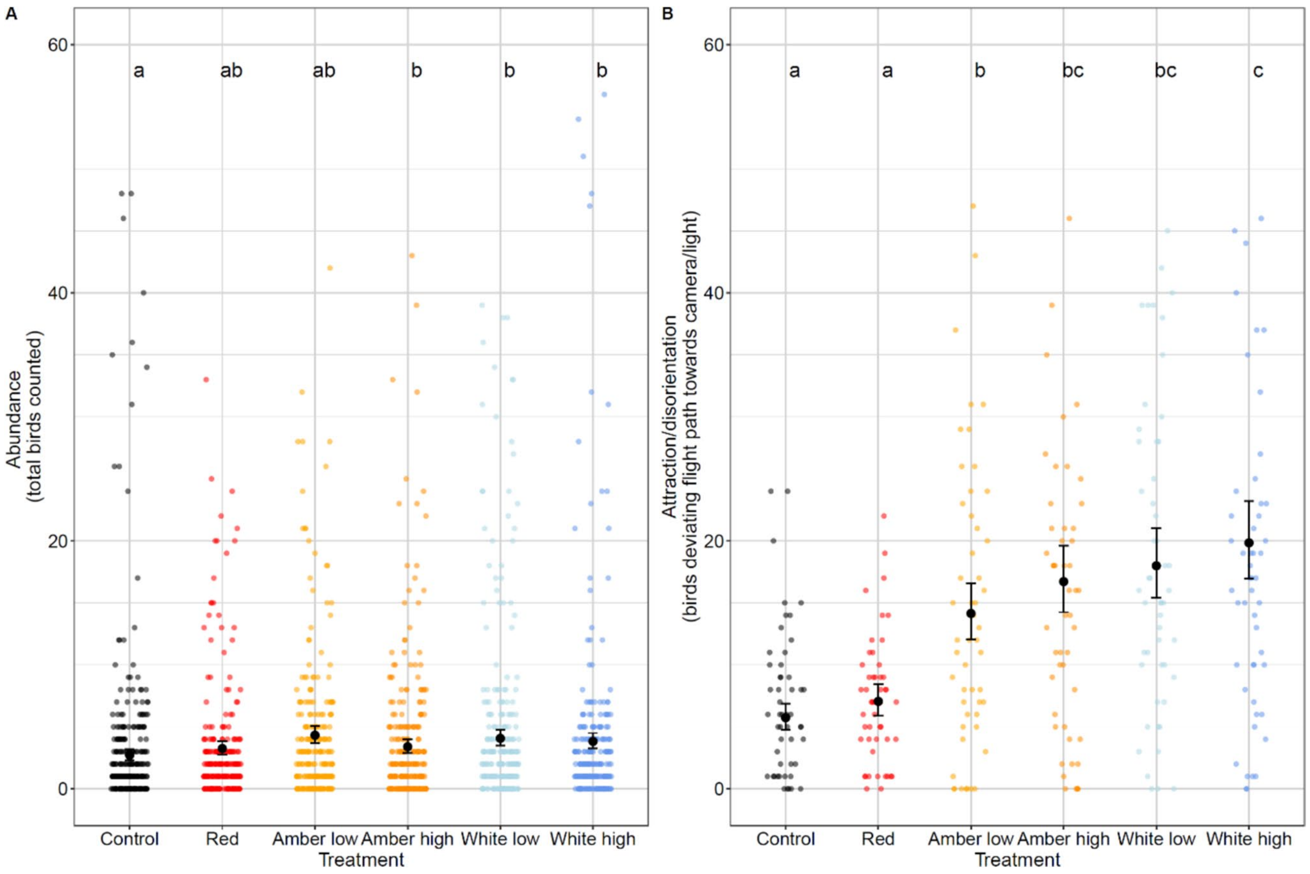

**Fig. 4** Raw data and estimated means and 95% confidence interval error bars f total birds counted at 10-s intervals (**A**) and birds counted deviating their flight path towards the camera/light per 1-min treatment period (**B**), where model estimates were computed using the top-ranking model offsets, average covariates, and back-transformed to the response scale. Different letters above treatments indicate significant differences between these treatments as determined by post hoc tests ($p \leq 0.05$)

**Table 1** Results from top-ranked models for the abundance and behaviour (attraction/disorientation), displaying, for those variables retained in the model, the incidence rate ratio (exponent of log incidence rate estimated by the models, using scaled predictors), 95% confidence interval (CI) of this ratio, and *p* value (bolded if $p \leq 0.05$)

| Predictors | Abundance | | | Attraction/disorientation | | |
|---|---|---|---|---|---|---|
| | Incidence rate ratios | CI | *p* | Incidence rate ratios | CI | *p* |
| Treatment | | | | | | |
| [Dark control] | 0.79 | 0.68–0.93 | **0.006** | 0.90 | 0.76–1.08 | 0.274 |
| [Red] | 0.95 | 0.81–1.12 | 0.554 | 1.11 | 0.93–1.33 | 0.242 |
| [Amber low] | 1.27 | 1.08–1.48 | **0.003** | 2.23 | 1.90–2.61 | **< 0.001** |
| [Amber high] | 0.99 | 0.85–1.17 | 0.944 | 2.64 | 2.25–3.09 | **< 0.001** |
| [White low] | 1.19 | 1.02–1.39 | **0.024** | 2.84 | 2.43–3.31 | **< 0.001** |
| [White high] | 1.12 | 0.95–1.32 | 0.163 | 3.13 | 2.67–3.66 | **< 0.001** |
| Moonlight intensity | 0.71 | 0.64–0.80 | **< 0.001** | 0.79 | 0.70–0.89 | **< 0.001** |
| Cloud cover | 1.11 | 1.03–1.21 | **0.010** | 1.07 | 0.99–1.17 | 0.101 |
| Wind northwards | 0.89 | 0.82–0.96 | **0.004** | | | |
| Time in treatment | 1.04 | 1.01–1.06 | **0.006** | | | |
| Relative humidity | | | | 1.23 | 1.11–1.36 | **< 0.001** |
| Wind speed | | | | 0.91 | 0.84–0.99 | **0.031** |
| Time since sunset | | | | 1.08 | 0.99–1.17 | 0.095 |

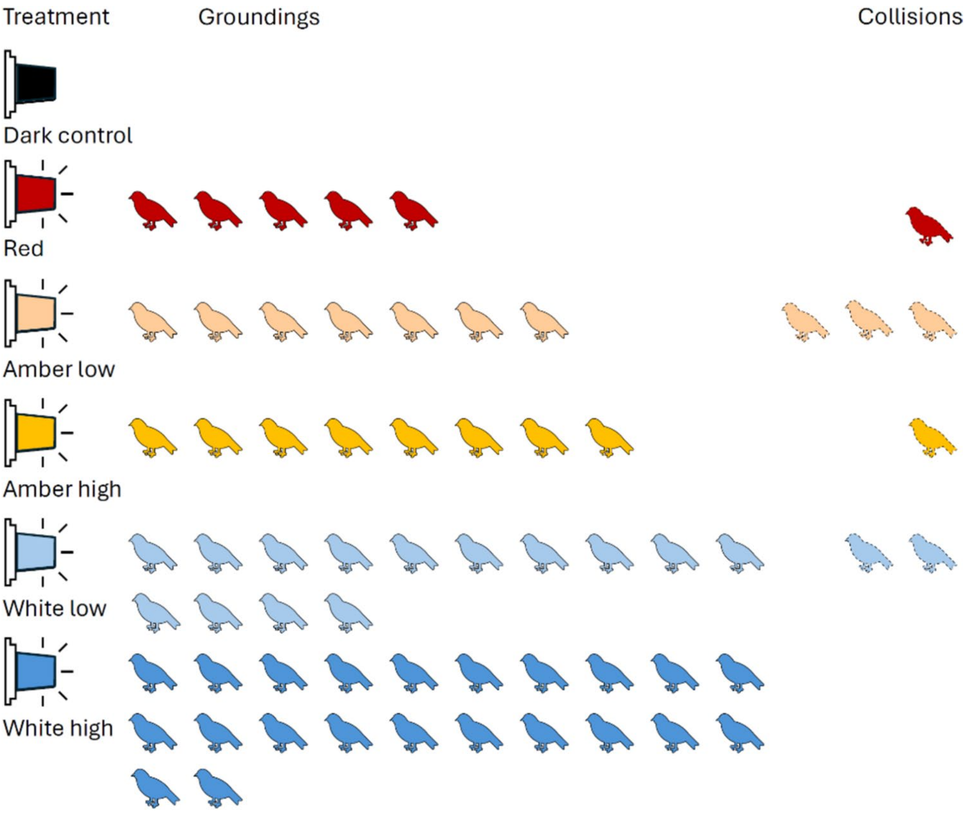

**Fig. 5** Number of grounded birds (left) and collisions with the lighting rig (right) per treatment across all study nights

**Table 2** Rated lumen outputs and spectral response indices for the light treatments, ranked by an increasing response index for rated output

| Light treatment | Rated output (lumens) | Spectral response index for 1 lm | Spectral response index for the rated output |
|---|---|---|---|
| Red | 4,800 | 0.667 | 3,202 |
| Amber low | 9,500 | 0.562 | 5,339 |
| Amber high | 19,000 | 0.562 | 10,678 |
| White low | 14,000 | 0.808 | 11,312 |
| White high | 28,000 | 0.808 | 22,624 |
| Reference (CIE D65 standard illuminant) | n/a | 1.000 | n/a |

## Discussion

Using an experiment assessing lighting impacts from different LED colours (red, amber, and white) and lumen outputs (brightness), we show that fairy prions are most impacted by white lights and high lumen output. Results showed a clear gradient in increasing attraction/disorientation of birds moving from red to white and at higher levels of brightness. Hence, specifically, warmer-coloured (red or amber) LEDs at reduced lumen outputs have the potential to help minimise seabird–vessel interactions. This supports previous work on other seabirds (Syposz et al. 2021). Whilst carried out on land, these findings will help inform seabird conservation efforts and highlight the need for mitigation measures, including the use of warmer LED colours operating at reduced lumen output to decrease vessel strikes (Rodriguez 2023). The impact of seabird–vessel attraction is of growing concern and poses a significant threat to many species (Fischer et al. 2021). Whilst not included in the current study, we highlight that an important aspect in the development of mitigation measures to reduce seabird–vessel interactions is the identification of, and compliance with, crew health and safety requirements around vessel lighting.

Our two different response measures (abundance and attraction/disorientation) showed qualitatively similar differences between light treatments. However, compared with the abundance counts of birds, patterns were stronger for the attraction/disorientation. When considering the impacts of ALAN, more direct measures of attraction/disorientation (such as interaction with the light beam) are likely more representative for assessing the risk of seabird–vessel interactions (i.e. seabird injury and/or mortality). We recommend that future work uses a camera with a field of view wider than the one used in the current study, as both of the above measures may have been underestimated, although we have no reason to believe that this would have resulted in biased estimates between treatments.

In addition to treatment effects, bird abundance and attraction/disorientation were also affected by environmental variables, including wind direction and speed, relative humidity, and moon illumination. This is consistent with other research on petrel species (Brown et al. 2023). More fairy prions were counted when the wind came more from the south, presumably because birds preferred to approach the island from this direction. Attraction/disorientation somewhat decreased with higher wind speed, consistent with another study on Procellariiformes (Bourgeois et al. 2008), but contrary to results in a study on fallout of shearwaters by Rodríguez et al. (2014). This is likely due to interspecific biological differences, including age, body mass, and wing strength/oscillation required for propulsion. Relative humidity was also strongly correlated with increased abundance and attraction/disorientation. Greater illumination of water particles in the air causing decreased visibility may have played a role in this. Similarly, assessing light-induced seabird–vessel interactions, Merkel and Johansen (2011) and Coleman et al. (2022) also found a strong correlation with high humidity, cloudy and foggy conditions, and poor visibility.

Lunar cycles drive animal behaviour (Bastos et al. 2022), which was supported by the inclusion of moonlight brightness in our models, where a brighter moon resulted in a lower abundance and fewer attracted/disorientated birds. A seabird rescue programme review by Rodríguez et al. (2023) included fledgling Procellariiformes, and the study hypothesised that anthropogenic lighting from sources such as vessels is less attractive or disorientating in clear sky conditions when the moon is bright. There have also been many studies investigating lunar effects on adult birds. Ravache et al. (2020) found that colony return rates in adult wedge-tailed shearwaters (*Ardenna pacifica*) did not alter under a full moon, whereas Mougeot and Bretagnolle (2000) found reduced colony attendance rates in non-breeder slender-billed prions *(Pachyptila belcheri*) on moonlit nights. Our study was conducted over 17 nights, which encompassed 1.5 lunar cycles. We recommend that future research focusses on increasing understanding of the combined effect of natural (moon) and anthropogenic light attraction/disorientation on adult seabirds.

We used an offset of bird abundance from the dark period immediately prior to treatment and found that the incorporation of time after sunset did not further improve the model fit for either response measure. Little is known about the impacts of lighting on fairy prion nocturnal arrival time or attendance rates to colonies, and these aspects were not included in the current study. Given that fairy prions are strongly attracted to at-sea vessel lights at night, we expected that they would be similarly attracted to anthropogenic lights originating at the colony. Our study differed from seabird light pollution research by Austad et al. (2023) on Yelkouan Shearwaters (*Puffinus yelkouan*), which measured attendance rates when the colony was illuminated by ship lights directed towards the colony, whereas we used a light source emanating directly from the colony. Their study showed that natural behaviour associated with nocturnal colony attendance was altered and hourly return rates were reduced by around 20% in the presence of anthropogenic lighting. Our results suggest that disorientation from ship lights may also play a role in colony attendance rates. It is commonly acknowledged that most nocturnal seabird species return to their burrows shortly after sunset to avoid visual detection by predators (Austad et al. 2023); however, illumination from moonlight also plays a key role in colony attendance patterns for species, including shearwaters, Procellariiformes (Rubolini et al. 2015).

Counts of grounded birds and collisions with the lighting rig showed a similar pattern to the modelled results, with increasing collisions and groundings for higher lumen outputs and whiter lights, albeit with a small sample size. Compared to other research investigating the impacts of lighting on seabirds (Rodríguez et al. 2017a), our study had low numbers of groundings and collisions. Since groundings are more common for fledglings (Rodríguez et al. 2017a), our study was designed to take place prior to chicks fledging, and hence only adults were included in the counts. It has been recognised that it is important to incorporate species-specific responses in assessing impacts of ALAN (Longcore et al. 2018; Longcore 2023), as this is the biologically relevant information for the species, rather than the colour spectrum perceived by humans. Less recognised is that the effects of lumen output are also incorporated, rather than spectrum alone. To address this, we used data from a closely related species in phylogeny and ecology and calculated the response in terms of an increase in brightness as likely experienced by the birds. Our results showed that the response of fairy prion to different light treatments is a combination of spectral response and intensity.

Whilst not measured in the current study, we theorise that non-breeders are effectively more active later at night and that it was these birds that were represented in increased counts. Further research would be needed to confirm this, while also considering the minor patterns in the model residuals. Secondly, our results may suggest a combination of the predator avoidance hypothesis (McNeil et al. 1993; Mougeot and Bretagnolle 2000) and adaptive behavioural plasticity (behavioural change in response to an external stimulus) (Mery and Burns 2010). Raw abundance counts were high when the treatments started (around 22:00 h) during the first three experimental nights. From experimental night 4 onwards, there were fewer fairy prion at the start of the treatments (Fig. S2). However, as our study was conducted on non-consecutive fair-weather nights, we could not assess whether prions became accustomed to the presence of lights and were therefore desensitised to the light treatment. This warrants further study.

Our study shows that bright lights within or close to colonies impact the behaviour of seabirds. This is of relevance to seabird colonies close to urban areas, as well as more remote locations that may be affected by lighting from vessels. We assume that behavioural responses to ALAN at the colony are similar to those at sea. Other studies in New Zealand show that seabirds are exposed to vessels with floodlights near their colony and that this risk varies during the breeding cycle, with the greatest exposure during courtship and post-guard (Fischer et al. 2021). In addition to other vessel attractants related to fishing activity, we suggest that floodlights, such as those used in our study, also act as an attractant to some seabirds and once in close proximity to the vessel it may cause them to become disorientated.

Overall, our results with fairy prion support findings in other published literature on seabird–artificial light interaction specifically those stating that reducing the lumen output and using non-white lights has the potential to help minimise seabird–vessel interactions (Syposz et al. 2021). In particular, warmer-coloured LEDs at reduced lumen outputs may be beneficial. Mitigation standards to reduce light-induced vessel interactions of seabirds with New Zealand commercial fishing vessels (DOC and MPI 2023) are supported by our results. We recommend that the following mitigation measures are considered for implementation internationally via vessel lighting management plans:

1. Undertake vessel-specific audits to determine lighting needs for different vessel operations. Light should only be provided when and where needed.
2. Use shielded luminaires, shaded windows, and non-reflective surfaces to minimise light spill and glare.
3. Ensure that the quality and level of light enables the vessel crew to operate safely. Factors such as colour rendering index (the ability to accurately show colours) may need to be considered.
4. Use low-lumen warm LEDs to minimise ecological impacts, especially in at-sea areas where seabird–vessel interaction is considered high risk.
5. Include breeding colony locations and timing of fledging periods within the vessel's area of operation in vessel lighting management plans. This will identify areas and times of year when it is desirable to operate vessels at reduced lighting where possible.

We recommend that future studies investigate red, amber, and white light with the same lumen output to cross-validate our results. Further work should also consider whether flicker from LED electronics impacts bird response (Inger et al. 2014). Additional land and sea-based studies will deepen our understanding of LED colour, lumen output, and time of night required to inform the selection of ecologically appropriate vessel lighting.

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**Author contributions** Project inception: JF. Methodology development: KM, DG, and JF. Lighting rig engineering: DG. Assembly: KM. Stephens's Island data collection: KM. Laboratory spectral analyses: SM. Data analyses: EC and DG. Manuscript writing and project management: KM, with important input from EC, DG, JF, and SM.

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**Data availability** The datasets analysed in the current study are held by DOC and will be available on request.

## Declarations

**Conflict of interest** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest and have no competing interests to declare that are relevant to the content of this article.

**Ethical statement** Experiments comply with the current laws of New Zealand. All research was led by the Department of Conservation, New Zealand, who hold statutory responsibilities for protected species conservation under the Wildlife Act (1953) and Conservation Act (1987).

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