

## RESEARCH ARTICLE

# Broad spectrum artificial light at night increases the conspicuousness of camouflaged prey

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Email: oak.mcmahon@plymouth.ac.uk**Funding information**Natural Environment Research Council,  
Grant/Award Number: NE/S003533/2**Handling Editor:** Mariana Mayer-Pinto**Abstract**

1. The growing global prevalence of energy efficient broad spectrum lighting threatens to disrupt an array of visually guided ecological processes. Broad spectrum lighting likely better enables the discrimination of colour, yet it is potential to increase the conspicuousness of camouflaged prey at night remains little explored.
2. Using a well-established visual model, we quantified the impacts of four spectrally distinct narrow and broad spectrum lighting technologies on the conspicuousness of three different polymorphic colour variations of intertidal littorinid snail, as viewed by three model predators.
3. Modern broad spectrum lighting technologies increased the conspicuousness of prey compared to 20th-century narrow spectrum lighting. This effect was most prominent in the yellow colour morphs due to greater contrast with their natural fucoid seaweed background.
4. *Synthesis and applications.* Our results provide evidence that the global transition to broad spectrum lighting will decrease the efficacy of camouflage at night in nature, potentially altering selective predation, population dynamics and the genetic structure of polymorphic populations. These findings highlight the need for further consideration in environmental management and planning, to ensure habitats are protected from unnecessary exposure to artificial light.

**KEYWORDS**

artificial light at night, artificial light spectra, camouflage, colour polymorphism, pollution, receptor noise limited model

## 1 | INTRODUCTION

The prevalence of artificial light at night (ALAN) has increased dramatically due to the expansion of urbanised areas worldwide (Falchi et al., 2016; Kyba et al., 2017). Estimates indicate that 23% of the world's surface between 75°N and 60°S is affected by ALAN (Falchi et al., 2016) with a rate of increase of 2.2% between 2012 and 2016 (Kyba et al., 2017). While these developments herald a new age of

simplicity in night time travel and security, an array of deleterious repercussions have been documented for humans and animals alike (Fonken & Nelson, 2014; Henn et al., 2014; Kempenaers et al., 2010; Santos et al., 2010; Thums et al., 2016).

As technologies develop, there has been a shift from narrow spectrum low-pressure sodium (LPS) towards luminaires that emit across a broader range of wavelengths (Davies et al., 2013; Elvidge et al., 2010), including high pressure sodium (HPS), metal halide (MH)

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and more recently light-emitting diodes (LED's) (Kyba et al., 2017). It is projected that LED bulbs will account for 85% of the global street lighting market by 2028 (Northeast Group LLC, 2019). Numerous concerns have been raised regarding the unforeseen ecological impacts of broad spectrum lighting (see Davies & Smyth, 2018 for an overview). Perhaps the most intuitive, yet little quantified of these impacts is the encroachment of light at night that enables colour guided behaviours previously only possible during the daytime (Briolat et al., 2021; Davies et al., 2013) or possibly under a full moon.

Camouflage is employed by a vast number of organisms to reduce conspicuousness. While methods of camouflage vary considerably, the most common strategy is known as background matching (Michalis et al., 2017), where an organism's colouration and patterning resembles its typical habitat. Cryptic colouration can dramatically alter conspicuousness and is an essential predator avoidance strategy in many species (Cheney et al., 2009; Cournoyer & Cohen, 2011; Stuart-Fox et al., 2003), particularly for sessile organisms that cannot rely on evasion. Many cryptic species exhibit polymorphic variations in their colouration, that can be selected for in spatially and temporally complex environments (Duarte et al., 2018). Given their selective disparity, the maintenance of varied colour morphs within a population is thought to be a complex phenomenon (Karpestam et al., 2016). Alongside stochastic processes such as genetic drift, it is thought small-scale environmental heterogeneity is predominantly responsible, where particular colourations are more resistant to thermal extremes or better able to background match and reduce conspicuousness to predators (Johannesson & Ekendahl, 2002; Phifer-Rixey et al., 2008).

The potential for broad spectrum lighting to impact the conspicuousness of camouflaged prey is clear. Such impacts may alter the balance of predator-prey interactions, population dynamics and the genetic structure of polymorphic populations. Its effect on the conspicuousness of camouflaged prey by predators at night have been little quantified (although see Briolat et al., 2021). Here, we provide evidence that a transition towards broad spectrum lighting can improve a predator's ability to discriminate prey species against a natural background. Our analysis spans three contrasting predator visual systems in the intertidal environment, with predation occurring both in air and in water accounting for the interaction of inherent optical water properties with the spectral composition of the artificial light field.

## 2 | MATERIALS AND METHODS

Using a well-established photoreceptor noise-limited chromatic discrimination model (Vorobyev & Osorio, 1998), we determine the conspicuousness of three statistically distinct colour morphs

of Littorinid snail (*Littorina obtusata* and *Littorina fabalis*) illuminated by 20th-century narrow spectrum lighting (LPS, and modern broad spectrum lighting (HPS; LEDs; and MH) as viewed by three different predators. Solar and lunar irradiances were also included in the model as natural reference points. This modelling approach has been used extensively to quantify the perceptibility of camouflaged prey species (Cournoyer & Cohen, 2011; Marshall et al., 2015; Stuart-Fox et al., 2003) and removes the risk of extraneous variables affecting predation that could arise experimentally. *L. obtusata* and *L. fabalis* are found commonly on fucoid macroalgae (*Fucus serratus*, *Fucus vesiculosus* and *Ascophyllum nodosum*) throughout the UK intertidal environment and exhibit a range of colour polymorphisms (yellow, olive and brown are most common) that help them reduce conspicuousness to predators against the fucoid macroalgae on which they live (Crothers, 2012). These snails are intertidal grazers of this macroalgae and are more active during the night when the risks of desiccation and predation are at their lowest. We selected three common predator models in temperate intertidal ecosystems that represented an array of differing predation modes and visual systems (Table 1). The herring gull *Larus argentatus* is a diurnal predator that forages for intertidal gastropods primarily while airborne and can discriminate complex colours using tetrachromatic vision (Crescitelli, 1958; Liebman, cited in Hart, 2001; Ödeen & Håstad, 2003). The impacts of ALAN on avian activity rhythms (Dominoni, 2015) and foraging strategies (Dwyer et al., 2013; Santos et al., 2010) allow *L. argentatus* to nocturnally hunt under man-made light sources. The common blenny *Lipophrys pholis* and green shore crab *Carcinus maenas* were selected as in water predators. *L. pholis* is a mostly diurnal predator and a trichromat capable of complex colour discrimination (Loew & Lythgoe, 1978). Nocturnal predation by fish in response to ALAN exposure is well documented (Becker et al., 2012; Bolton et al., 2017). *C. maenas* is a mostly nocturnal predator (Silva et al., 2010) and a dichromat less able to discriminate a broad range of colours from a background (Martin & Mote, 1982).

### 2.1 | Data acquisition and initial processing

The receptor noise model established by Vorobyev and Osorio (1998) was used to determine the discernibility of prey against their background by a number of predator species. This model relies upon three key parameters: (a) the reflectance spectra of prey species and the background on which they typically reside; (b) the spectral sensitivities of each photoreceptor possessed by a predator; and (c) the irradiance spectrum of light striking the prey individual and the background against which it is camouflaged.

Predator	$\lambda_{\max}$ (nm)	Source
Herring Gull	371, 447, 503, 568	Crescitelli (1958), Liebman, cited in Hart (2001) and Ödeen and Håstad (2003)
Common Blenny	500, 535, 570	Loew and Lythgoe (1978)
Green Shore Crab	440, 508	Martin and Mote (1982)

TABLE 1 The  $\lambda_{\max}$  values used to model the spectral sensitivities of the herring gull, common blenny and green shore crab

In all, 67 *L. fabalis* and *L. obtusata* individuals were collected from the fucoïd macroalgae, *Fucus vesiculosus*, using fifteen 30 cm quadrats in May 2020, along the mid-tide gullies of the Portwrinkle section of Whitsand Bay 50°21'N, 4°18'W, South West U.K. Both species are most commonly found on *F. vesiculosus*, however can occur on other species including *Fucus serratus* and *Ascophyllum nodosum*. Each group of *Littorina* were divided into pots based on the quadrat they were sampled from. Hyperspectral reflectance spectra were quantified ex situ in sunlight using an Ocean Insight OCEAN-HDX-XR spectrometer with a wavelength response from 200 to 1,100 nm, fitted with a 3 m long 1,000  $\mu\text{m}$  fibre optic probe. The spectrometer was calibrated before each pot was measured using a WS-1-SL Spectralon® Diffuse Reflectance Standard. Measurements were taken at the top of their shell along the last whirl, holding the fibre-optic probe at a 5 mm distance above each individual and pointing down. Shells were air-dried prior to measurement reducing specular reflection. Two measurements were also taken from the frond and vesicle of the seaweed *F. vesiculosus*, which were averaged to create a single, representative background reflectance spectrum. *F. vesiculosus* was selected as a model background as *Littorina* species are known to favourably reside upon fucoïd macroalgae where they can employ cryptic background matching (Johannesson & Ekendahl, 2002). All reflectance spectra were standardised to a 1 nm resolution through averaging, and readings outside of the 350–750 nm range were omitted. The averaged reflectance spectra for the three colour morphs of littorinid snail and background algae are given in Figure 1c. Ethical approval was not required as no animals were removed from their native environment and no invasive, stressful or harmful procedures were performed.

To determine different colour morphs, *Littorina* were classified visually into Brown, Olive and Citrine (Yellow) classifications using a colour scheme presented by Rolán-Alvarez et al. (2012). No orange specimens were found ( $n = 35$  Brown,  $n = 15$  Olive,  $n = 17$  Yellow). The number of individuals per morph allowed replication for the receptor noise model and statistical analysis. These qualitative classifications were validated statistically using Multivariate Analysis of Variance performed on a Bray–Curtis dissimilarity matrix calculated from the raw reflectance data using CRAN: VEGAN (Oksanen et al., 2007) in R v3.6.1 (R Core Team, 2020). Prior to use in the receptor noise model, the raw *Littorina* reflectance spectra were smoothed by a parameter of 0.2 using the 'prospec' function of the R package 'PAVO 2' (Maia et al., 2019), to remove unwanted electrical noise.

## 2.2 | Modelling predator visual systems

An extensive literature search was carried out to locate each predator's lambda max ( $\lambda_{\text{max}}$ ) values, the wavelength at which each photoreceptor maximally absorbs light (Table 1). We were unable to source spectral sensitivity data measured specifically from the

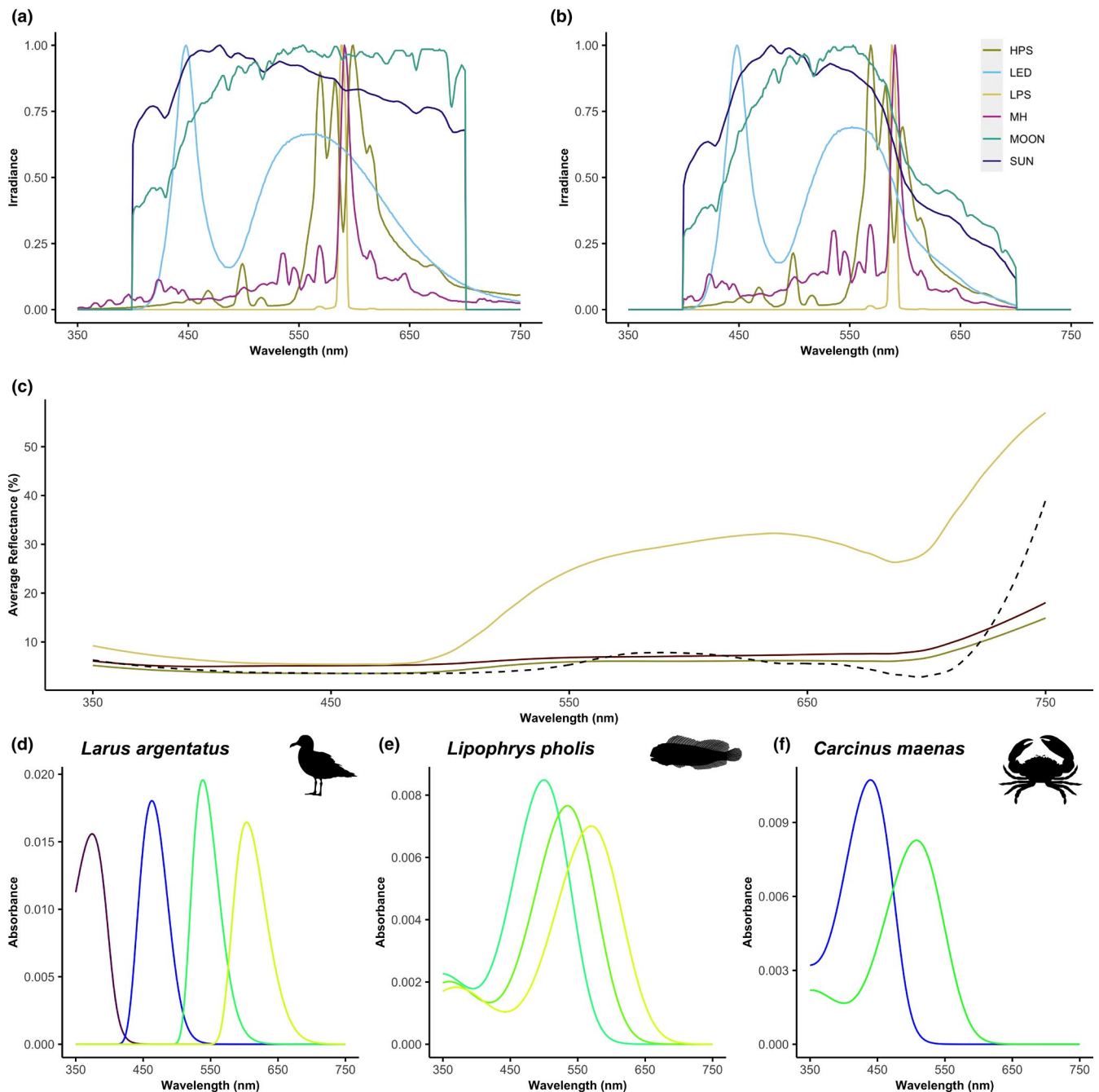
Herring Gull. Where spectral sensitivities for UV sensitive (UVS) avian species have been unavailable in the past, many studies utilise the sensitivities of the blue tit *Cyanistes caeruleus* as a model for an average UVS bird (Avilés, 2008; Håstad et al., 2005). To reinforce the validity of the herring gull results in our study, the majority of its photoreceptor absorbance curves are derived from published sensitivities from the Laridae family (Crescitelli, 1958; Liebman, cited in Hart, 2001; Ödeen & Håstad, 2003). Therefore, our herring gull visual model represents the best possible approximation. The modelled absorbance spectra of the photoreceptors in the eyes of each model predator are given in Figure 1d–f.

Hyperspectral irradiance measurements previously collected by Davies et al. (2013) at a 1 nm resolution between 350 and 750 nm (MAYA2000 Pro) were used to represent the environmental light spectrum under each lighting technology (LPS, HPS, LED and MH). Conspicuousness was also modelled under sunlight and moonlight to provide natural light sources for comparison. Sea surface solar irradiances were collected from the L4 buoy of the Western Channel Observatory (50.250°N; 4.217°W) at midday on June 24th 2014 under clear sky conditions using an Satlantic Hyperspectral Radiometer. Lunar irradiances were downloaded from: (<http://www.olino.org/blog/us/articles/2015/10/05/spectrum-of-moon-light>). Measurements were made using a SpecBos 1211 spectroradiometer (51.424°N, 5.409°E) and collected during a clear full moon night on the 14th April 2014.

The street lighting technologies represent an assortment of artificial light sources that were used in the 20th and 21st centuries and each possess a unique spectral composition, with LPS lighting typically emitting narrow spectrum irradiance at 590 nm (Davies et al., 2014) and HPS, LED and MH emitting across a broader spectral range. HPS emits yellow/orange light similar to LPS although across a broader spectrum. LED lighting typically has wavelength peaks in the blue and green range (Elvidge et al., 2010), while MH is able to emit light within the UV range (Davies et al., 2013). Measurements were collected from urban lighting installations around Cornwall, U.K. at ground level to accurately record the irradiance that animals are exposed to. It was assumed fish and crab predators viewed *Littorina* while submerged. To account for the different attenuations of artificial light wavelengths in seawater, irradiance spectra for their models were obtained using the HYDROLIGHT radiative transfer numerical model to simulate the passage of light from each source through 3 m of water (i.e. 3 m depth) with a chlorophyll concentration of 0.3  $\text{mg}/\text{m}^{-3}$ . HYDROLIGHT output ranged between 400 and 700 nm, with values between 350 and 400 nm and 700 and 750 nm set to zero. In air and in water, irradiance spectra for each light source are given in Figure 1a and b, respectively.

## 2.3 | Visual modelling

The visual modelling section of the experiment was carried out using CRAN: pavo 2 (Maia et al., 2019).



**FIGURE 1** Spectra used to parametrise visual modelling of the conspicuous of littorinid snail colour morphs to three visual predators. (a) In air, relative irradiances used in models for the herring gull *Larus argentatus*. Irradiances have been scaled to between 0 and 1 to facilitate comparison of contrasting spectral compositions. (b) Model in water relative irradiances (3 m depth) used to parametrise models for the common blenny *Lipophrys pholis* and shore crab *Carcinus maenas*. (c) Averaged reflectance spectrum collected from yellow, olive and brown morphs of *Littorina obtusata* and *Littorina fabalis*. The averaged reflectance spectrum for the fucoid algae background is given as a dashed black line. (d–f) The modelled spectral absorbance curves of the photoreceptors in the eyes of each visual predator

The spectral absorbance curves of each predator's photoreceptors were modelled from their  $\lambda_{\max}$  values using the standard visual pigment template of Govardovskii et al. (2000) and Hart and Vorobyev (2005). For the herring gull, this function required the input of  $\lambda_{\text{cut}}$ ,  $B_{\text{mid}}$  and ocular media transmission data, owing to their more complex visual system involving cone oil droplets.  $\lambda_{\text{cut}}$

values were estimated using the average of all available avian values from Hart and Vorobyev (2005). *pavo 2*'s standard ocular media transmission for avian visual systems, 'bird' (Hart & Vorobyev, 2005), was also used. In the absence of  $B_{\text{mid}}$  data, the *oiltype* argument was used to calculate  $B_{\text{mid}}$  using regression equations from Hart and Vorobyev (2005).

Quantum catch values for each photoreceptor were then calculated using the *vismodel* function which integrates the spectral absorbance curves with the reflectance of the prey subject and its background, and the hyperspectral irradiance of the lighting technology being tested. Quantum catch refers to the proportion of photons that are captured by each receptors photopigment when viewing a subject. A total of 36 outputs were created, to obtain data for the three polymorphs as perceived by the three predators under the four lighting conditions. As in previous studies on colour discrimination, a von Kries adaptation coefficient was applied to each visual model to account for colour constancy in different lighting conditions (Cournoyer & Cohen, 2011; Siddiqi et al., 2004). The averaged background reflectance spectra of *Fucus vesiculosus* and each lighting technologies irradiance data were also included in this calculation. Each visual model's relative argument was set to FALSE to obtain raw photon catches that are suitable for use in *pavo* 2's *coldist* function (Maia et al., 2019).

For all 36 *vismodel* outputs, Euclidean colour distances ( $\Delta S$ ) were calculated in units of Just Noticeable Difference (JND) between prey and background quantum catches using the *coldist* function. JND values greater than 1 approximate the minimum level at which prey can be perceived (Bitton et al., 2019; Cournoyer & Cohen, 2011) with higher values indicating a stronger contrast between the prey and their natural background. To obtain colour distances, photoreceptor densities must be input and quantum catches must be weighed against the Weber fraction (noise-to-signal ratio) of the cones. It was assumed the herring gull and common blenny have a Weber fraction of 0.1 and 0.05, respectively, based on known avian and fish values (Olsson et al., 2017). For the crab, we have followed widely used protocols for unavailable data and used a Weber fraction of 0.05 (Bitton et al., 2019; Cournoyer & Cohen, 2011; Matz et al., 2006) as median estimate of published data that range between 0.02 in humans and 0.1 in some birds (Matz et al., 2006). For the herring gull's photoreceptor proportions, we used values that represent an average UVS bird (1:2:2:4) utilised by Seymoure et al. (2019). This is an accurate estimation as gull species are known to have a high proportion of long wavelength sensitive (LWS) cones (Hart, 2001). The common blenny's proportions were based on those typically seen in diurnal percomorphs (1:2:2), with a single cone surrounded by four double cones (Ali & Anctil, 1976; White et al., 2004). Due to unavailable data, the shore crab's proportions were set to 1:1, maximising its ability for colour discrimination (Lettieri et al., 2009). While this approximation may affect the magnitude of absolute values obtained from the model, the relationship between them will be maintained (Cheney et al., 2009; Lettieri et al., 2009), meaning that the relationships and contrasts between light types and colour morphs within each predator modelled in our study will still be valid. We cannot, however, make statistical comparisons on the effect of artificial lighting between the predators. Neural values were calculated using the noise argument as described by previous artificial lighting experiments (Ronald et al., 2017), indicating bright conditions and a high photoreceptor saturation.

## 2.4 | Statistical analysis

Exceptionally, low JND values obtained for LPS in comparison to other lighting technologies produced a highly skewed response variable distribution that did not conform to normality even following log transformation. JND response values were instead investigated using generalised linear models fitted with a gamma error distribution. A two-way analysis of variance was performed on each predator's JND response values to quantify whether the four artificial light sources significantly impacted the conspicuousness of each of the three *Littorina* colour morphs. Pairwise contrasts were performed using the *EMMEANS* package's (Lenth et al., 2019) *contrast* function to determine significant differences in colour distance between each light source and colour morph's  $\Delta S$  values. The Tukey method was applied as a *p* value adjustment to control for inflated type II errors when performing a modest number of multiple tests.

## 3 | RESULTS

The classification of Littorinid snail colour morphs into Brown, Olive and Yellow was validated using a multivariate analysis of variance performed on a Bray–Curtis dissimilarity matrix calculated from the raw reflectance data of each individual (MANOVA:  $F_{2,64} = 35$ ,  $p < 0.001$ ; Figure S1). While this validated our classification, a clear distinction can be made between the reflectance spectra of yellow from other colour morphs (Figure 1c). Olive and brown morphs exhibited similar reflectance spectra (Figure 1c) and displayed no clear clustering in the MDS ordination (Figure S1) suggesting that these may actually be one variable 'dark morph'. An extensive review of currently proposed classification systems is beyond the scope of this paper; hence, our analysis is based on the classification of Rolán-Alvarez et al. (2012). Further reflectance data across multiple shores are needed before an informed appraisal of current classification systems can be made.

The ability of all three predators to discriminate the three colour morphs against a fucoid algae background was significantly different depending on which light source was used (Herring Gull: Gamma GLM,  $\chi^2_{6256} = 0.063$ ,  $p = <0.001$ ; Common Blenny: Gamma GLM,  $\chi^2_{6256} = 0.1472$ ,  $p = <0.001$ ; Green Shore Crab, Gamma GLM,  $\chi^2_{6256} = 0.5669$ ,  $p = <0.001$ ). Pairwise comparisons of the conspicuousness of the colour morphs are presented by predator for each artificial and natural light source in Tables S1–S3, summarised in Table 2 and presented visually in Figure 2.

The JND values of all three prey morphs remained below the minimum threshold of detectability (1) under LPS lighting (Figure 2). As such, all three predators are unlikely to be able to differentiate any colour morph from the fucoid algae background when illuminated with LPS lighting, rendering any statistical differences in JND ecologically meaningless. The threshold of detectability was exceeded to varying degrees under the broader spectrum (HPS, LED and MH) light sources, sunlight and the full moon. The shift to broader spectrum (MH, HPS and LED) lighting, however, increases

	Herring gull	Common blenny	Shore crab
Visual system	Tetrachromatic	Trichromatic	Dichromatic
Medium	Air	Water	Water
HPS	Y > B > O	Y = B > O; O = Y	Y > B > O
LED	Y > B > O	Y = B > O	Y > B = O
LPS	Y < B = O	Y < B = O	Y < B = O; O = Y
MH	Y > B = O	Y < B = O	Y > B = O
SUN	Y > B = O	Y > B > O	Y > B = O
MOON	Y > B = O	Y = B > O	Y > B = O

Notes: Colour morphs to the left of '>' are significantly more conspicuous than those to the right at the 95% confidence level. Colour morphs separated by '=' do not significantly differ in conspicuousness to predators at the 95% confidence level.

the conspicuousness of some colour morphs more than others, depending on the predator (Figure 2).

When illuminated by LED, MH, the sun or the moon, yellow colour morphs were significantly more conspicuous to herring gulls (Figures 2a and 3a; Table 2; Table S1) and shore crabs (Figures 2c and 3c; Table 2; Table S3) compared to brown and olive morphs. This was also the case when illuminated by HPS lighting, except brown morphs were also more conspicuous than olive.

The switch to broad spectrum lighting had a lesser impact on the conspicuousness of the three colour morphs to the common blenny (Figures 2b and 3b; Table 2; Table S2). In sunlight, yellow colour morphs were most conspicuous, while in moonlight and LED light, yellow and brown colour morphs were equally more conspicuous than olive. When illuminated by HPS lighting, brown morphs were more conspicuous than olive but not yellow, and yellow morphs were equally as conspicuous as olive. When illuminated with MH lighting, brown colour morphs were significantly more conspicuous than yellow but not olive morphs, while olive and yellow morphs were equally as conspicuous.

## 4 | DISCUSSION

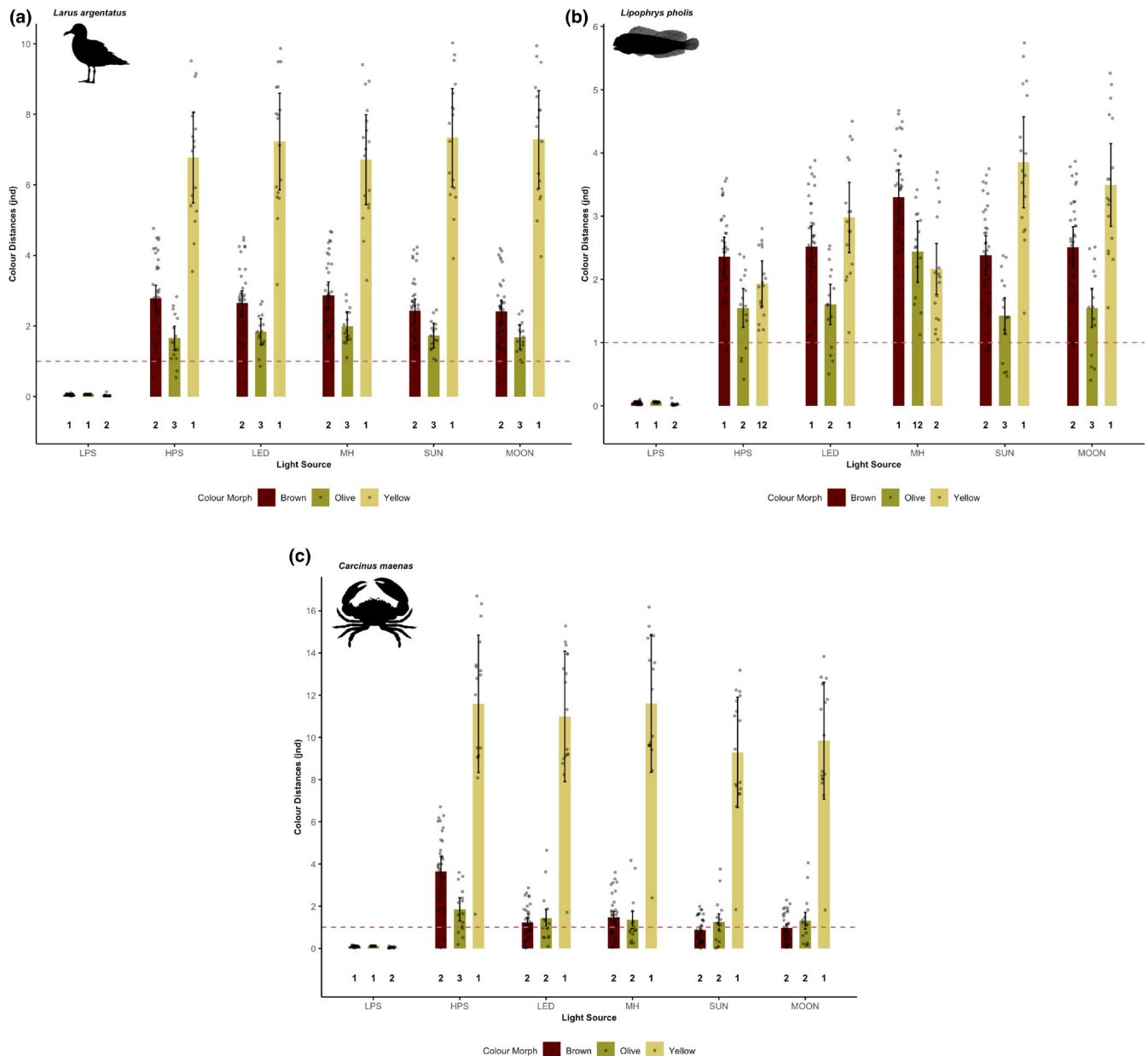
While ALAN's ability to increase predation pressure on prey populations (Becker et al., 2012; Bennie et al., 2018; Bolton et al., 2017; Frank, 1988; Underwood et al., 2017) is now well documented, few studies have so far evaluated its potential to inhibit cryptic background matching by camouflaged prey (Briolat et al., 2021). The results of this study indicate that broader spectrum lighting technologies (HPS, LED and MH) increase the conspicuousness of prey species at night by reducing the efficacy of cryptic background matching when compared to narrow spectrum lighting. This may have profound implications for the fitness of cryptic species that rely on camouflage for their survival (Coker et al., 2009; Imperio et al., 2013). It should be noted however, that while prey species may be more conspicuous under broad spectrum lighting, conspicuousness does not necessarily scale linearly with colour distance (Santiago et al., 2020). Further behavioural research is needed to verify the suprathresholds of JND at which prey items become

conspicuous to predators; however, these were beyond the scope of this initial research. Nonetheless, littorinid prey remained under the threshold of detectability when illuminated by LPS lighting at night, and above this threshold when illuminated by modern broad spectrum lighting indicating that they have become detectable to predators at night where LPS lighting has been replaced.

The magnitude of broad spectrum lighting's effect on the conspicuousness of prey was largely dependent on the colour morph being perceived. While some variability was observed, Yellow *Littorina* were commonly more affected by broader spectrum lighting sources (HPS, LED and MH), likely owing to the greater distinction between their spectral reflectance and that of the *Fucus vesiculosus* background. This suggests that polymorphic colour variations that do not employ background matching techniques may be selectively preyed upon when illuminated by broad spectrum light, leading to altered population structure. Broad spectrum ALAN could therefore have impacts on the structure of polymorphic populations similar those seen on the peppered moth *Biston betularia* in the UK during the early 20th century (Cook, 2003). This would lead to greater homogeneity in polymorphic populations affected by broad spectrum ALAN, where more conspicuous colourations have been extirpated through enhanced predation or forced to migrate to habitats better suited for crypsis. Similar trends have been documented in a variety of species in response to habitat changes brought on by climate change (Delhey & Peters, 2017; Jones et al., 2020; Roulin, 2014). This may also have a deleterious effect on species that exhibit garish colouration for sexual display at the expense of crypsis (Keren-Rotem et al., 2016), further exacerbating population decline by increasing the predation risk of viable mates.

In all predators studied, a shift from LPS to broader light types (HPS, LED and MH) increased the ability to perceive prey. This is likely because the broader spectral composition stimulates the multiple photoreceptors of predators (Davies et al., 2013), enhancing colour discrimination through visual opponent mechanisms that rely on the differences between receptor signals (Cournoyer & Cohen, 2011; Vorobyev & Brandt, 1997). While each of the broad light sources provoked a largely similar response in most cases, some notable differences were found between predator responses

TABLE 2 The impact of contrasting lighting sources on the comparative conspicuousness of yellow (Y), Brown (B) and olive (O) colour morphs of intertidal littorinid snail (*Littorina obtusata*/*Littorina fabalis*) to three predators with contrasting visual systems that hunt in air or water. Summarised from Tables S3–S6

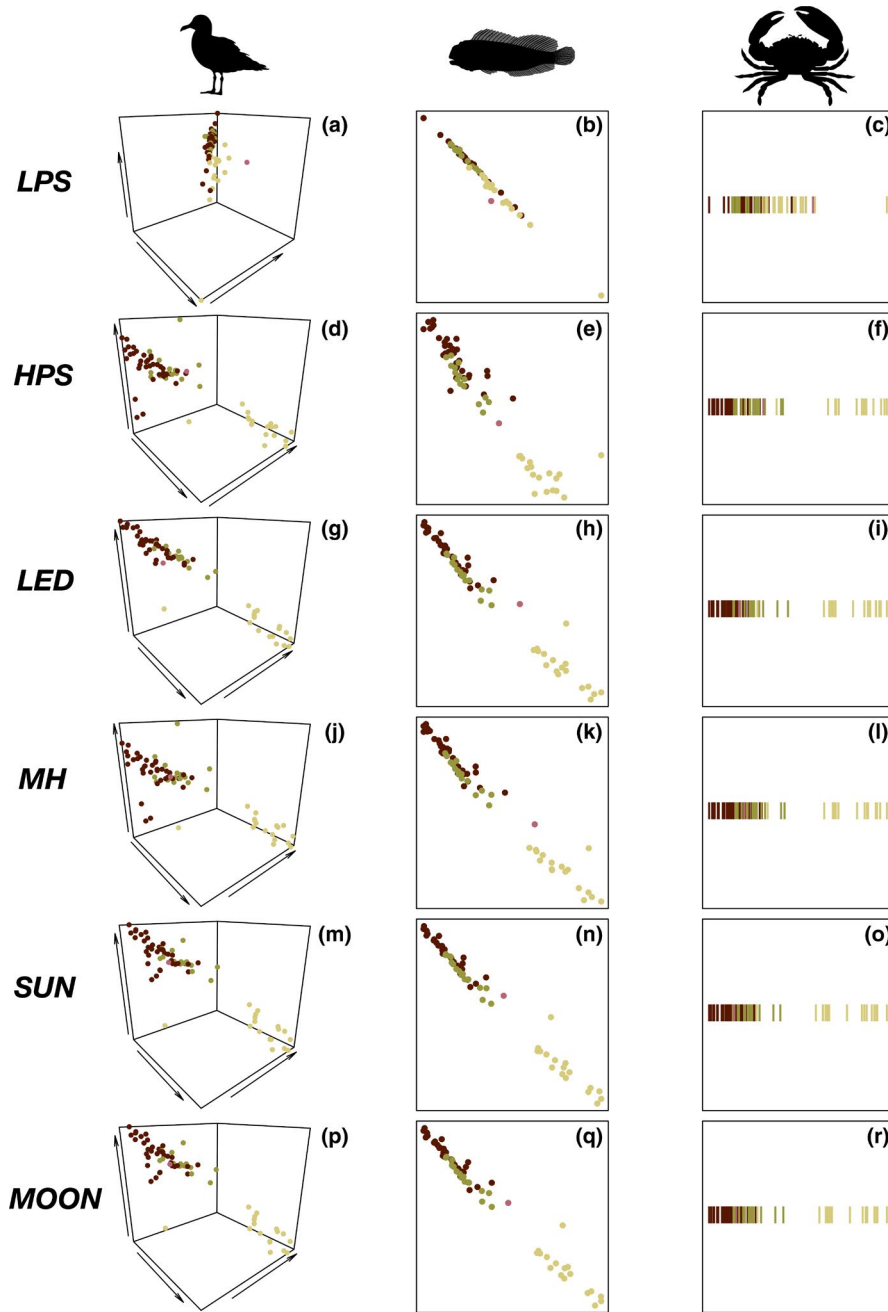


**FIGURE 2** The impact of four alternative lighting technologies on the conspicuousness of three different colour morphs of intertidal littorinid snail to three predators with contrasting colour vision systems. Plot is derived from colour distance data indicating the chromatic contrast between *Littorina* and its natural background, as viewed by a predator. Bars represent model mean values, error bars represent 95% confidence limits. Grey dots represent raw *Littorina* colour distance values. Numbers in bold indicate significant differences between the effects of each light type at the 95% confidence level, where numbers differ within each colour morph grouping (see Tables S1–S3 for results of pairwise contrasts). The dashed line indicates 1 JND, the minimum threshold of detectability. Where these numbers are shared within a colour morph group, no significant difference can be inferred

under different lighting technologies. It is likely that these differences would be more prominent if a broader selection of predator species were studied, given the diverse range of photoreceptor sensitivities that can be exhibited. For instance, visually guided behaviours in predators with spectral sensitivities that extend further into shorter UV wavelengths such as lizards, arachnids and reptiles will likely be most affected by MH technologies that can emit light in the UV range (Davies et al., 2013). The short wavelength, blue peak in LED lighting will also be more likely than other light types to affect

marine organisms as it can penetrate further into the ocean (Davies et al., 2014).

The impact of broad spectrum lighting on conspicuousness is also variable between receivers. When viewed by the common blenny for example, the relative conspicuousness of yellow colour morphs was not as impacted by broad spectrum lighting compared to the herring gull and shore crab. This is likely because the photoreceptors of the common blenny are more tightly clustered and centred on the green portion of spectrum (Figure 1e). When



**FIGURE 3** The impact of various light sources on the colour distances between camouflaged prey and their background by intertidal predators. Colour distances between yellow, olive and brown colour morphs of *Littorina obtusata* and *Littorina fabalis* as perceived by the tetrachromatic herring gull *Larus argentatus* (a, d, g, j, m, p), the trichromatic common blenny *Lipophrys pholis* (b, e, h, k, n, q) and the dichromatic shore crab *Carcinus maenas* (c, f, i, l, o, r) under low-pressure sodium (a–c), high-pressure sodium (d–f), LED (g–i), MH (j–l) outdoor lighting technologies. Colour distances between different morphs illuminated by the sun (m, n, o) and moon (p, q, r) are also provided. Red points represent the fucoid algae background

attempting to interpolate the real-world outcomes of visual models, multiple predators and their relative impacts on prey populations need to be accounted for.

The potential ecological repercussions that arise from the proliferation of modern broad spectrum lighting have been discussed at length (Davies et al., 2013; Davies & Smyth, 2018; Gaston et al., 2012), many of which arise from the facilitation of visually guided behaviours previously limited to the day (Davies et al., 2013). A variety of mitigation methods are available for planners and environmental managers when considering the ecological impacts of ALAN. These include reducing the amount of light used, shielding lights to prevent spill into the surrounding environment, part night lighting during times of peak demand and manipulating the spectra of lighting to minimise ecological

impacts (Gaston et al., 2012). Given that broad spectrum lighting facilitates colour discrimination by predators and consequently increases the conspicuousness of prey, it is intuitive to suggest using narrow spectrum lighting to avoid these impacts. In the absence of colour however, nocturnal predators will use luminance contrast perception. We suggest a review of the colour vision systems of nocturnal predators in a given ecosystem should be undertaken to identify those wavelengths of light that minimise luminance contrast perception of prey items against backgrounds. Managers should remain aware however, that the impacts of ALAN extend beyond those on camouflage to impact all aspects of organism biology, and that all parts of the visual spectrum will likely have some ecological impact (Davies & Smyth, 2018).



This study has demonstrated that broad spectrum artificial lighting has the potential to increase the conspicuousness of camouflaged prey species at night and leave colour variations with less effective background matching at greater risk of predation. If selective predation of colour morphs is sufficiently affected by the proliferation of LED lighting (Kyba et al., 2017), this could reduce prey populations and alter the genetic structure of naturally polymorphic populations.

## ACKNOWLEDGEMENT

This work was supported by the Natural Environment Research Council (grant number NE/S003533/2 awarded to T.W.D. and T.S.).

## CONFLICT OF INTEREST

None to declare.

## AUTHORS' CONTRIBUTIONS

O.M. and T.W.D. designed the study; O.M. conducted the visual modelling, analysis and wrote the first draft of the manuscript; T.W.D. carried out the fieldwork and provided guidance throughout the experiment; T.W.D. provided irradiance data gathered from his 2013 study; T.S. implemented the optical model of light attenuation in seawater. All authors contributed to revisions.

## DATA AVAILABILITY STATEMENT

The data supporting these findings are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.5hqbkzkh7h> (McMahon et al., 2022).

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## REFERENCES

- Ali, M. A., & Anctil, M. (1976). *Retinas of fishes: An atlas*. Springer Berlin Heidelberg.
- Avilés, J. M. (2008). Egg colour mimicry in the common cuckoo *Cuculus canorus* as revealed by modelling host retinal function. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2345–2352.
- Becker, A., Whitfield, A. K., Cowley, P. D., Järnegren, J., & Næsje, T. F. (2012). Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology*, 50, 43–50.
- Bennie, J., Davies, T. W., Cruse, D., Inger, R., & Gaston, K. J. (2018). Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *Journal of Applied Ecology*, 55, 2698–2706.
- Bitton, P. P., Yun Christmann, S. A., Santon, M., Harant, U. K., & Michiels, N. K. (2019). Visual modelling supports the potential for prey detection by means of diurnal active photolocation in a small cryptobenthic fish. *Scientific Reports*, 9, 8089.
- Bolton, D., Mayer-Pinto, M., Clark, G. F., Dafforn, K. A., Brassil, W. A., Becker, A., & Johnston, E. L. (2017). Coastal urban lighting has ecological consequences for multiple trophic levels under the sea. *Science of the Total Environment*, 576, 1–9.
- Briolat, E. S., Gaston, K. J., Bennie, J., Rosenfeld, E. J., & Troscianko, J. (2021). Artificial nighttime lighting impacts visual ecology links between flowers, pollinators and predators. *Nature Communications*, 12, 4163.
- Cheney, K. L., Skogh, C., Hart, N. S., & Marshall, N. J. (2009). Mimicry, colour forms and spectral sensitivity of the bluestriped fangblenny, *Plagiotremus rhinorhynchos*. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1565–1573.
- Coker, D. J., Pratchett, M. S., & Munday, P. L. (2009). Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology*, 20, 1204–1210.
- Cook, L. M. (2003). The rise and fall of the Carbonaria form of the peppered moth. *The Quarterly Review of Biology*, 78, 399–417.
- Cournoyer, B. L., & Cohen, J. H. (2011). Cryptic coloration as a predator avoidance strategy in seagrass shrimp colormorphs. *Journal of Experimental Marine Biology and Ecology*, 402, 27–34.
- Crescitelli, F. (1958). The natural history of visual pigments. *Annals of the New York Academy of Sciences*, 74, 230–255.
- Crothers, J. (2012). *Snails on rocky shores*. Pelagic Publishing.
- Davies, T. W., Bennie, J., Inger, R., de Ibarra, N. H., & Gaston, K. J. (2013). Artificial light pollution: Are shifting spectral signatures changing the balance of species interactions? *Global Change Biology*, 19, 1417–1423.
- Davies, T. W., Duffy, J. P., Bennie, J., & Gaston, K. J. (2014). The nature, extent, and ecological implications of marine light pollution. *Frontiers in Ecology and the Environment*, 12, 347–355.
- Davies, T. W., & Smyth, T. (2018). Why artificial light at night should be a focus for global change research in the 21st century. *Global Change Biology*, 24, 872–882.
- Delhey, K., & Peters, A. (2017). Conservation implications of anthropogenic impacts on visual communication and camouflage. *Conservation Biology*, 31, 30–39.
- Domironi, D. (2015). The effects of light pollution on biological rhythms of birds: An integrated, mechanistic perspective. *Journal of Ornithology*, 156, 1–10.
- Duarte, R. C., Stevens, M., & Flores, A. A. V. (2018). The adaptive value of camouflage and colour change in a polymorphic prawn. *Scientific Reports*, 8, 16028.
- Dwyer, R. G., Bearhop, S., Campbell, H. A., & Bryant, D. M. (2013). Shedding light on light: Benefits of anthropogenic illumination to a nocturnally foraging shorebird. *Journal of Animal Ecology*, 82, 478–485.
- Elvidge, C. D., Keith, D. M., Tuttle, B. T., & Baugh, K. E. (2010). Spectral identification of lighting type and character. *Sensors*, 10, 3961–3988.
- Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., Portnov, B. A., Rybnikova, N. A., & Furgoni, R. (2016). The new world atlas of artificial night sky brightness. *Science Advances*, 2, e1600377.
- Fonken, L. K., & Nelson, R. J. (2014). The effects of light at night on circadian clocks and metabolism. *Endocrine Reviews*, 35, 648–670.
- Frank, K. D. (1988). Impact of outdoor lighting on moths an assessment. *Journal of the Lepidopterists' Society*, 42, 63–93.
- Gaston, K. J., Davies, T. W., Bennie, J., & Hopkins, J. (2012). Reducing the ecological consequences of night-time light pollution: Options and developments. *Journal of Applied Ecology*, 49, 1256–1266.
- Govardovskii, V. I., Fyhrquist, N., Reuter, T., Kuzmin, D. G., & Donner, K. (2000). In search of the visual pigment template. *Visual Neuroscience*, 17, 509–528.
- Hart, N. S. (2001). The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research*, 20, 675–703.
- Hart, N. S., & Vorobyev, M. (2005). Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *Journal of Comparative Physiology A*, 191, 381–392.
- Håstad, O., Ernstdotter, E., & Ödeen, A. (2005). Ultraviolet vision and foraging in dip and plunge diving birds. *Biology Letters*, 1, 306–309.
- Henn, M., Nichols, H., Zhang, Y., & Bonner, T. H. (2014). Effect of artificial light on the drift of aquatic insects in urban Central Texas streams. *Journal of Freshwater Ecology*, 29, 307–318.

- Imperio, S., Bionda, R., Viterbi, R., & Provenzale, A. (2013). Climate change and human disturbance can lead to local extinction of alpine rock ptarmigan: New insight from the Western Italian Alps. *PLoS ONE*, *8*, e81598.
- Johannesson, K., & Ekendahl, A. (2002). Selective predation favouring cryptic individuals of marine snails (Littorina). *Biological Journal of the Linnean Society*, *76*, 137–144.
- Jones, M. R., Mills, L. S., Jensen, J. D., & Good, J. M. (2020). Convergent evolution of seasonal camouflage in response to reduced snow cover across the snowshoe hare range. *Evolution*, *74*, 2033–2045.
- Karpestam, E., Merilaita, S., & Forsman, A. (2016). Colour polymorphism protects prey individuals and populations against predation. *Scientific Reports*, *6*, 22122.
- Kempnaers, B., Borgström, P., Loës, P., Schlicht, E., & Valcu, M. (2010). Artificial night lighting affects Dawn song, extra-pair siring success, and lay date in songbirds. *Current Biology*, *20*, 1735–1739.
- Keren-Rotem, T., Levy, N., Wolf, L., Bouskila, A., & Geffen, E. (2016). Male preference for sexual signalling over crypsis is associated with alternative mating tactics. *Animal Behaviour*, *117*, 43–49.
- Kyba, C. C. M., Kuester, T., Sánchez de Miguel, A., Baugh, K., Jechow, A., Hölker, F., Bennie, J., Elvidge, C. D., Gaston, K. J., & Guanter, L. (2017). Artificially lit surface of earth at night increasing in radiance and extent. *Science Advances*, *3*, e1701528.
- Lenth, R., Buerkner, P., Herve, M., Love, J., Riebl, H., & Singmann, H. (2019). *Emmeans: Estimated marginal means, aka least-squares means*. R package version 1.7.0. Retrieved from <https://CRAN.R-project.org/package=emmeans>
- Lettieri, L., Cheney, K. L., Mazel, C. H., Boothe, D., Marshall, N. J., & Strelman, J. T. (2009). Cleaner gobies evolve advertising stripes of higher contrast. *Journal of Experimental Biology*, *212*, 2194–2203.
- Loew, E. R., & Lythgoe, J. N. (1978). The ecology of cone pigments in teleost fishes. *Vision Research*, *18*, 715–722.
- Maia, R., Gruson, H., Endler, J. A., & White, T. E. (2019). Pavo 2: New tools for the spectral and spatial analysis of colour in r. *Methods in Ecology and Evolution*, *10*, 1097–1107.
- Marshall, K. L. A., Philpot, K. E., Damas-Moreira, I., & Stevens, M. (2015). Intraspecific colour variation among lizards in distinct Island environments enhances local camouflage. *PLoS ONE*, *10*, e0135241.
- Martin, F. G., & Mote, M. I. (1982). Color receptors in marine crustaceans: A second spectral class of reticular cell in the compound eyes of Callinectes and Carcinus. *Journal of Comparative Physiology*, *145*, 549–554.
- Matz, M. V., Marshall, N. J., & Vorobyev, M. (2006). Are corals colorful? *Photochemistry and Photobiology*, *82*, 345–350.
- McMahon, O., Smyth, T., & Davies, T. W. (2022). Data from: Broad spectrum artificial light at night increases the conspicuousness of camouflaged prey. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.5hqbzkh7h>
- Michalis, C., Scott-Samuel, N. E., Gibson, D. P., & Cuthill, I. C. (2017). Optimal background matching camouflage. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170709.
- Northeast Group LLC. (2019) *Global smart street lighting & smart cities: Market forecast (2019–2028)*. Technical Report 4849803.
- Ödeen, A., & Håstad, O. (2003). Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution*, *20*, 855–861.
- Oksanen, J., Kindt, R., Legendre, P., & O'Hara, B. (2007) *Vegan: Community ecology package*. R package version 1.8-5. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Olsson, P., Lind, O., & Kelber, A. (2017). Chromatic and achromatic vision: Parameter choice and limitations for reliable model predictions. *Behavioural Ecology*, *29*, 273–282.
- Phifer-Rixey, M., Heckman, M., Trussell, G. C., & Schmidt, P. S. (2008). Maintenance of clinal variation for shell colour phenotype in the flat periwinkle *Littorina obtusata*. *Journal of Evolutionary Biology*, *21*, 966–978.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Rolán-Alvarez, E., Saura, M., Diz, A. P., José Rivas, M., Alvarez, M., Cortés, B., Coo, A., Estévez, D., & Iglesias, L. (2012). Can sexual selection and disassortative mating contribute to the maintenance of a shell color polymorphism in an intertidal marine snail? *Current Zoology*, *58*, 463–474.
- Ronald, K. L., Ensminger, A. L., Shawkey, M. D., Lucas, J. R., & Fernández-Juricic, E. (2017). Testing a key assumption in animal communication: Between-individual variation in female visual systems alters perception of male signals. *Biology Open*, *6*, 1771–1783.
- Roulin, A. (2014). Melanin-based colour polymorphism responding to climate change. *Global Change Biology*, *20*, 3344–3350.
- Santiago, C., Green, N. F., Hamilton, N., Endler, J. A., Osorio, D. C., Marshall, N. J., & Cheney, K. L. (2020). Does conspicuousness scale linearly with colour distance? A test using reef fish. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20201456.
- Santos, C. D., Miranda, A. C., Granadeiro, J. P., Lourenço, P. M., Saraiva, S., & Palmeirim, J. M. (2010). Effects of artificial illumination on the nocturnal foraging of waders. *Acta Oecologica*, *36*, 166–172.
- Seymour, B. M., Linares, C., & White, J. (2019). Connecting spectral radiometry of anthropogenic light sources to the visual ecology of organisms. *Journal of Zoology*, *308*, 93–110.
- Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M., & Summers, K. (2004). Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology*, *207*, 2471–2485.
- Silva, A. C. F., Hawkins, S. J., Boaventura, D. M., Brewster, E., & Thompson, R. C. (2010). Use of the intertidal zone by mobile predators: Influence of wave exposure, tidal phase and elevation on abundance and diet. *Marine Ecology Progress Series*, *406*, 197–210.
- Stuart-Fox, D. M., Moussalli, A., Marshall, N. J., & Owens, I. P. F. (2003). Conspicuous males suffer higher predation risk: Visual modelling and experimental evidence from lizards. *Animal Behaviour*, *66*, 541–550.
- Thums, M., Whiting, S. D., Reisser, J., Pendoley, K. L., Pattiaratchi, C. B., Proietti, M., Hetzel, Y., Fisher, R., & Meekan, M. G. (2016). Artificial light on water attracts turtle hatchlings during their near shore transit. *Royal Society Open Science*, *3*, 160142.
- Underwood, C. N., Davies, T. W., & Queirós, A. M. (2017). Artificial light at night alters trophic interactions of intertidal invertebrates. *Journal of Animal Ecology*, *86*, 781–789.
- Vorobyev, M., & Brandt, R. (1997). How do insect pollinators discriminate colors? *Israel Journal of Plant Sciences*, *45*, 103–113.
- Vorobyev, M., & Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society B: Biological Sciences*, *265*, 351–358.
- White, E. M., GonCalves, D. M., Partridge, J. C., & Oliveira, R. F. (2004). Vision and visual variation in the peacock blenny. *Journal of Fish Biology*, *65*, 227–250.

## SUPPORTING INFORMATION

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**How to cite this article:** McMahon, O., Smyth, T. & Davies, T. W. (2022). Broad spectrum artificial light at night increases the conspicuousness of camouflaged prey. *Journal of Applied Ecology*, 00, 1–10. <https://doi.org/10.1111/1365-2664.14146>