

2022-03-25

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<http://hdl.handle.net/10026.1/18654>

10.1111/1365-2664.14146

Journal of Applied Ecology

Wiley

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1 Broad spectrum artificial light at night increases the conspicuousness of 2 camouflaged prey

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9

10

11 Abstract

12 1. The growing global prevalence of energy efficient broad spectrum lighting
13 threatens to disrupt an array of visually guided ecological processes. Broad
14 spectrum lighting likely better enables the discrimination of colour, yet it's
15 potential to increase the conspicuousness of camouflaged prey at night remains
16 little explored.

17 2. Using a well-established visual model, we quantified the impacts of four
18 spectrally distinct narrow and broad spectrum lighting technologies on the
19 conspicuousness of three different polymorphic colour variations of intertidal
20 littorinid snail, as viewed by three model predators.

21 3. Modern broad spectrum lighting technologies increased the conspicuousness of
22 prey compared to 20th century narrow spectrum lighting. This effect was most
23 prominent in the yellow colour morphs due to greater contrast with their natural
24 fucoid seaweed background.

25 4. *Synthesis & Applications.* Our results provide evidence that the global transition
26 to broad spectrum lighting will decrease the efficacy of camouflage at night in
27 nature, potentially altering selective predation, population dynamics and the
28 genetic structure of polymorphic populations. These findings highlight the need
29 for further consideration in environmental management and planning, to ensure
30 habitats are protected from unnecessary exposure to artificial light.

31

32 **Keywords:** camouflage, artificial light spectra, ALAN, colour polymorphism, receptor
33 noise limited model, pollution.

34

35 Introduction

36 The prevalence of Artificial Light at Night (ALAN) has increased dramatically due to the
37 expansion of urbanised areas worldwide (Falchi et al., 2016; Kyba et al., 2017).

38 Estimates indicate that 23% of the world's surface between 75°N and 60°S is affected
39 by ALAN (Falchi et al., 2016) with a rate of increase of 2.2% between 2012 and 2016
40 (Kyba et al., 2017). While these developments herald a new age of simplicity in night
41 time travel and security, an array of deleterious repercussions have been documented
42 for humans and animals alike (Kempnaers et al., 2010; Santos et al., 2010; Fonken &
43 Nelson, 2014; Henn et al., 2014; Thums et al., 2016).

44 As technologies develop, there has been a shift from narrow spectrum low-pressure
45 sodium (LPS) towards luminaires that emit across a broader range of wavelengths
46 (Elvidge et al., 2010; Davies et al., 2013), including High Pressure Sodium (HPS), Metal
47 Halide (MH), and more recently Light Emitting Diodes (LED's) (Kyba et al., 2017). It is
48 projected that LED bulbs will account for 85% of the global street lighting market by
49 2028 (Northeast Group LLC, 2019). Numerous concerns have been raised regarding
50 the unforeseen ecological impacts of broad spectrum lighting (see Davies & Smyth,
51 2018 for an overview). Perhaps the most intuitive, yet little quantified of these impacts is
52 the encroachment of light at night that enables colour guided behaviours previously only
53 possible during the daytime (Davies *et al.* 2013; Briolat et al. 2021) or possibly under a
54 full moon.

55 Camouflage is employed by a vast number of organisms to reduce conspicuousness.
56 While methods of camouflage vary considerably, the most common strategy is known
57 as background matching (Michalis et al., 2017), where an organisms colouration and
58 patterning resembles its typical habitat. Cryptic colouration can dramatically alter

59 conspicuousness and is an essential predator avoidance strategy in many species
60 (Stuart-Fox et al., 2003; Cheney et al., 2009; Cournoyer & Cohen., 2011), particularly
61 for sessile organisms that cannot rely on evasion. Many cryptic species exhibit
62 polymorphic variations in their colouration, that can be selected for in spatially and
63 temporally complex environments (Duarte et al., 2018). Given their selective disparity,
64 the maintenance of varied colour morphs within a population is thought to be a complex
65 phenomenon (Karpestam et al., 2016). Alongside stochastic processes such as genetic
66 drift, it is thought small scale environmental heterogeneity is predominantly responsible,
67 where particular colourations are more resistant to thermal extremes or better able to
68 background match and reduce conspicuousness to predators (Johannesson &
69 Ekendahl, 2002; Phifer-Rixey et al., 2008).

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

80 Methods

81 Using a well established photoreceptor noise-limited chromatic discrimination model
82 (Vorobyev & Osario, 1998), we determine the conspicuousness of three statistically
83 distinct colour morphs of Littorinid snail (*Littorina obtusata* and *Littorina fabalis*)
84 illuminated by 20th century narrow spectrum lighting (Low Pressure Sodium (LPS)], and
85 modern broad spectrum lighting [High Pressure Sodium (HPS); Light Emitting Diodes
86 (LEDs); and Metal Halide (MH)] as viewed by three different predators. Solar and lunar
87 irradiances were also included in the model as natural reference points. This modelling
88 approach has been used extensively to quantify the perceptibility of camouflaged prey

89 species (Stuart-Fox et al., 2005; Cournoyer & Cohen, 2011; Marshall et al., 2015) and
90 removes the risk of extraneous variables affecting predation that could arise
91 experimentally. *L. obtusata* and *L. fabalis* are found commonly on furoid macroalgae
92 (*Fucus serratus*, *Fucus vesiculosus* and *Ascophyllum nodosum*) throughout the UK
93 intertidal environment and exhibit a range of colour polymorphisms (yellow, olive and
94 brown are most common) that help them reduce conspicuousness to predators against
95 the furoid macroalgae on which they live (Crothers 2012). These snails are intertidal
96 grazers of this macroalgae, and are more active during the night when the risks of
97 desiccation and predation are at their lowest. We selected three common predator
98 models in temperate intertidal ecosystems that represented an array of differing
99 predation modes and visual systems (Table 1). The herring gull (*Larus argentatus*) is a
100 diurnal predator foraging for intertidal gastropods primarily in air and can discriminate
101 complex colours using tetrachromatic vision (Crescitelli, 1958; Liebman, cited in Hart,
102 2001; Hart, 2001; Ödeen & Håstad, 2003). ALAN has demonstrated impacts on avian
103 activity rhythms (Dominoni 2015) and foraging strategies (Santos et al. 2010; Dwyer et
104 al. 2013) that make nocturnal predation of *L. argentatus* under man-made light sources
105 possible. The common blenny (*Lipophrys pholis*) and green shore crab (*Carcinus*
106 *maenas*) were selected as in water predators. *L. pholis* is a mostly diurnal predator and
107 a trichromat capable of complex colour discrimination (Loew & Lythgoe, 1978).
108 nocturnal predation by fish in response to ALAN exposure is well documented (Becker
109 et al. 2013; Bolton et al. 2017). *C. maenas* is a mostly nocturnal predator (Silva et al.
110 2010) and a dichromat less able to discriminate a broad range of colours from a
111 background (Martin & Mote, 1982).

112

113 *Data Acquisition & Initial Processing*

114 The receptor noise model established by Vorobyev and Osario (1998) was used to
115 determine the discernibility of prey against their background by a number of predator
116 species. This model relies upon three key parameters: 1) the reflectance spectra of prey
117 species and the background on which they typically reside; 2) the spectral sensitivities
118 of each photoreceptor possessed by a predator; and 3) the irradiance spectrum of light
119 striking the prey individual and the background against which it is camouflaged.

120 Sixty seven *L. fabalis* and *L. obtusata* individuals were collected from the fucoid
121 macroalgae, *Fucus vesiculosus*, using fifteen 30cm quadrats in May 2020, along the
122 mid-tide gullies of the Portwrinkle section of Whitsand Bay 50°21'N, 4°18'W, South
123 West U.K. Both species are most commonly found on *F. vesiculosus*, however can
124 occur on other species including *Fucus serratus* and *Ascophyllum nodosum*. Each
125 group of *Littorina* were divided into pots based on the quadrat they were sampled from.
126 Hyperspectral reflectance spectra were quantified ex situ in sunlight using an Ocean
127 Insight OCEAN-HDX-XR spectrometer with a wavelength response from 200-1100nm,
128 fitted with a 3m long 1000µm fibre optic probe. The spectrometer was calibrated before
129 each pot was measured using a WS-1-SL Spectralon® Diffuse Reflectance Standard.
130 Measurements were taken at the top of their shell along the last whirl, holding the fibre-
131 optic probe at a 5mm distance above each individual and pointing down. Shells were air
132 dried prior to measurement reducing specular reflection. Two measurements were also
133 taken from the frond and vesicle of the seaweed *F. vesiculosus*, which were averaged
134 to create a single, representative background reflectance spectrum. *F. vesiculosus* was
135 selected as a model background as *Littorina* species are known to favourably reside
136 upon fucoid macroalgae where they can employ cryptic background matching
137 (Johannesson & Eken Dahl, 2002). All reflectance spectra were standardised to a 1nm
138 resolution through averaging, and readings outside of the 350nm-750nm range were
139 omitted. The averaged reflectance spectra for the three colour morphs of littorinid snail
140 and background algae are given in Figure 1C. Ethical approval was not required as no
141 animals were removed from their native environment and no invasive, stressful or
142 harmful procedures were performed.

143 To determine different colour morphs, *Littorina* were classified visually into Brown, Olive
144 and Citrine (Yellow) classifications using a colour scheme presented by Rolán-Alvarez
145 et al., (2012), as no orange specimens were found ($n = 35$ Brown, $n = 15$ Olive, $n = 17$
146 Yellow). The number of individuals per morph allowed replication for the receptor noise
147 model and statistical analysis. These qualitative classifications were validated
148 statistically using Multivariate Analysis of Variance performed on a Bray-Curtis
149 dissimilarity matrix calculated from the raw reflectance data using CRAN: Vegan
150 (Oksanen et al., 2007) in R v3.6.1 (R Core Team, 2020). Prior to use in the receptor

151 noise model, the raw *Littorina* reflectance spectra were smoothed by a parameter of 0.2
152 using the 'prospec' function of the R package 'pavo 2' (Maia et al., 2019), to remove
153 unwanted electrical noise.

154 *Modelling Predator Visual Systems*

155 An extensive literature search was carried out to locate each predator's lambda max
156 (λ_{max}) values, the wavelength at which each photoreceptor maximally absorbs light
157 (Table 1). We were unable to source spectral sensitivity data measured specifically from
158 the Herring Gull. Where spectral sensitivities for UV sensitive (UVS) avian species have
159 been unavailable in the past, many studies utilise the sensitivities of the blue tit
160 (*Cyanistes caeruleus*) as a model for an average UVS bird (Håstad et al., 2005; Avilés,
161 2008). To reinforce the validity of the herring gull results in our study, the majority of its
162 photoreceptor absorbance curves are derived from published sensitivities from the
163 Laridae family (Crescitelli, 1958; Liebman, cited in Hart, 2001; Hart, 2001; Ödeen &
164 Håstad, 2003). Therefore, our herring gull visual model represents the best possible
165 approximation. The modelled absorbance spectra of the photoreceptors in the eyes of
166 each model predator are given in Figure 1 D-F.

167 Hyperspectral irradiance measurements previously collected by Davies et al. (2013) at a
168 1nm resolution between 350-750nm (MAYA2000 Pro) were used to represent the
169 environmental light spectrum under each lighting technology (LPS, HPS, LED, MH).
170 Conspicuousness was also modelled under sunlight and moonlight to provide natural
171 light sources for comparison. Sea surface solar irradiances were collected from the L4
172 buoy of the Western Channel Observatory (50.250°N; 4.217°W) at midday on June 24th
173 2014 under clear sky conditions using an Satlantic Hyperspectral Radiometer. Lunar
174 irradiances were downloaded from
175 (<http://www.olino.org/blog/us/articles/2015/10/05/spectrum-of-moon-light>).

176 Measurements were made using a SpecBos 1211 spectroradiometer (51.424°N,
177 5.409°E) and collected during a clear full moon night on the 14th April 2014.

178 The street lighting technologies represent an assortment of artificial light sources that
179 were used in the 20th and 21st century and each possess a unique spectral

180 composition, with LPS lighting typically emitting narrow spectrum irradiance at 590nm
181 (Davies et al., 2014) and HPS, LED and MH emitting across a broader spectral range.
182 HPS emits yellow/orange light similar to LPS although across a broader spectrum. LED
183 lighting typically has wavelength peaks in the blue and green range (Elvidge et al.,
184 2010), while MH is able to emit light within the UV range (Davies et al., 2013).
185 Measurements were collected from urban lighting installations around Cornwall, U.K. at
186 ground level to accurately record the irradiance that animals are exposed to. It was
187 assumed fish and crab predators viewed *Littorina* while submerged. To account for the
188 different attenuations of artificial light wavelengths in seawater, irradiance spectra for
189 their models were obtained using the HYDROLIGHT radiative transfer numerical model
190 to simulate the passage of light from each source through 3m of water (i.e. 3m depth)
191 with a chlorophyll concentration of 0.3 mg m⁻³. HYDROLIGHT output ranged between
192 400nm-700nm, with values between 350nm-400nm and 700nm-750nm set to zero. In
193 air and in water irradiance spectra for each light source are given in Figure 1 A and B
194 respectively.

195 *Visual Modelling*

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

198 The spectral absorbance curves of the photoreceptors in the eyes of each predator
199 were modelled from their λ_{max} values using the standard visual pigment template of
200 Govardovskii et al. (2000) and Hart & Vorobyev (2005). For the herring gull, this function
201 required the input of λ_{cut} , *Bmid* and ocular media transmission data, owing to their more
202 complex visual system involving cone oil droplets. λ_{cut} values were estimated using the
203 average of all available avian values from Hart & Vorobyev (2005). *Pavo 2*'s standard
204 ocular media transmission for avian visual systems, "bird" (Hart et al., 2005), was also
205 used. In the absence of *Bmid* data, the *oiltype* argument was used to calculate *Bmid*
206 using regression equations from Hart & Vorobyev (2005).

207 Quantum catch values for each photoreceptor were then calculated by using the
208 vismodel function which integrates the spectral absorbance curves with the reflectance

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

220 For all 36 vismodel outputs, Euclidean colour distances (ΔS) were calculated in units of
221 Just Noticeable Difference (JND) between prey and background quantum catches using
222 the coldist function. JND values greater than 1 approximate the minimum level at which
223 a single (prey) can be perceived (Cournoyer & Cohen, 2011; Bitton, 2019) with higher
224 values indicating a stronger contrast between the prey and their natural background. To
225 obtain colour distances, photoreceptor densities must be input and quantum catches
226 must be weighted against the Weber fraction (noise-to-signal ratio) of the cones. It was
227 assumed the herring gull and common blenny have a Weber fraction of 0.1 and 0.05
228 respectively, based on known avian and fish values (Olsson et al., 2017). For the crab,
229 we have followed widely used protocols for unavailable data and used a Weber fraction
230 of 0.05 (Matz et al., 2006; Cournoyer & Cohen, 2011; Bitton et al., 2019) as median
231 estimate of published data that range between 0.02 in humans to 0.1 in some birds
232 (Matz et al., 2006). For the herring gull's photoreceptor proportions, we used values that
233 represent an average UVS bird (1:2:2:4) utilised by Seymoure et al. (2019) in a similar
234 experiment. This is an accurate estimation as gull species are known to have a high
235 proportion of long wavelength sensitive (LWS) cones (Hart, 2001). The common
236 blenny's proportions were based on those typically seen in diurnal percomorphs (1:2:2),
237 with a single cone surrounded by four double cones (Ali & Anctil, 1976; White et al.,
238 2004). Due to unavailable data, the shore crab's proportions were set to 1:1, maximising
239 its ability for colour discrimination (Lettieri et al., 2009). While this approximation may

240 affect the magnitude of absolute values obtained from the model, the relationship
241 between them will be maintained (Cheney et al., 2009; Lettieri et al., 2009), meaning
242 that the relationships and contrasts between light types and colour morphs within each
243 predator modelled in our study will still be valid. We cannot, however, make statistical
244 comparisons on the effect of artificial lighting between the predators. Neural values
245 were calculated using the noise argument as described by previous artificial lighting
246 experiments (Ronald et al., 2017), indicating bright conditions and a high photoreceptor
247 saturation.

248 *Statistical Analysis*

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

261 **Results**

262 The classification of Littorinid snail colour morphs into Brown, Olive and Yellow was
263 validated using a multivariate analysis of variance performed on a Bray-Curtis
264 dissimilarity matrix calculated from the raw reflectance data of each individual
265 (MANOVA: $F_{2,64} = 35$, $P < 0.001$) (Supplementary Figure 1). While this validated our
266 classification, a clear distinction can be made between the reflectance spectra of yellow
267 from other colour morphs (Figure 1C). Olive and brown morphs exhibited similar
268 reflectance spectra (Figure 1C) and displayed no clear clustering in the MDS ordination
269 (Figure S1) suggesting that these may actually be one variable 'dark morph'. An

270 extensive review of currently proposed classification systems is beyond the scope of
271 this paper, hence our analysis is based on the classification of Rolán-Alvarez *et al.*,
272 (2012). Further reflectance data across multiple shores is needed before an informed
273 appraisal of current classification systems can be made.

274 The ability of all three predators, to discriminate the three colour morphs against a
275 fucoid algae background was significantly different depending on which light source was
276 used (Herring Gull: Gamma GLM, $\chi^2_{6,256} = 0.063$, $P = <0.001$; Common Blenny:
277 Gamma GLM, $\chi^2_{6,256} = 0.1472$, $P = <0.001$; Green Shore Crab, Gamma GLM, $\chi^2_{6,256} =$
278 0.5669 , $P = <0.001$). Pairwise comparisons of the conspicuousness of the colour
279 morphs are presented by predator for each artificial and natural light source in
280 Supplementary Tables 1-3, summarised in Table 2 and presented visually in Figure 2.

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

290 When illuminated by LED, MH, the sun or the moon, yellow colour morphs were
291 significantly more conspicuous to herring gulls (Figures 2A and 3A, Table 2,
292 Supplementary Table 1) and shore crabs (Figure 2C and 3C, Table 2, Supplementary
293 Table 3) compared to brown and olive morphs. This was also the case when illuminated
294 by HPS lighting, except brown morphs were also more conspicuous than olive.

295 The switch to broad spectrum lighting had a lesser impact on the conspicuousness of
296 the three colour morphs to the common blenny (Figures 2B and 3B, Table 2,
297 Supplementary Table 2). In sunlight, yellow colour morphs were most conspicuous,
298 while in moonlight and LED light, yellow and brown colour morphs were equally more

299 conspicuous than olive. When illuminated by HPS lighting, brown morphs were more
300 conspicuous than olive, but not yellow, and yellow morphs were equally as conspicuous
301 as olive. When illuminated with MH lighting, brown colour morphs were significantly
302 more conspicuous than yellow but not olive morphs, while olive and yellow morphs were
303 equally as conspicuous.

304 Discussion

305 While ALAN is now well documented to increase predation pressure on prey
306 populations (Frank 1988; Becker *et al.* 2012; Bolton *et al.* 2017; Underwood, Davies &
307 Queirós 2017; Bennie *et al.* 2018), few studies have so far evaluated its potential to
308 inhibit cryptic background matching by camouflaged prey (Briolat *et al.* 2021). The
309 results of this study indicate that broader spectrum lighting technologies (HPS, LED and
310 MH) increase the conspicuousness of prey species at night by reducing the efficacy of
311 cryptic background matching when compared to narrow spectrum lighting. This may
312 have profound implications for the fitness of cryptic species that rely on camouflage for
313 their survival (Coker *et al.*, 2009; Imperio *et al.*, 2013). It should be noted however, that
314 while prey species may be more conspicuous under broad spectrum lighting,
315 conspicuousness does not necessarily scale linearly with colour distance (Santiago *et*
316 *al.* 2020). Further behavioural research is needed to verify the suprathresholds of JND
317 at which prey items become conspicuous to predators, however these were beyond the
318 scope of this initial research. Nonetheless, littorinid prey remained under the threshold
319 of detectability when illuminated by LPS lighting at night, and above this threshold when
320 illuminated by modern broad spectrum lighting indicating that they have become
321 detectable to predators at night where LPS lighting has been replaced.

322 The magnitude of broad spectrum lighting's effect on the conspicuousness of prey was
323 largely dependent on the colour morph being perceived. While some variability was
324 observed, Yellow *Littorina* were most commonly more affected by broader spectrum
325 lighting sources (HPS, LED, MH), likely owing to the greater distinction between their
326 spectral reflectance and that of the *Fucus vesiculosus* background. This suggests that
327 polymorphic colour variations that do not employ background matching techniques may
328 be selectively preyed upon when illuminated by broad spectrum light, leading to altered

329 population structure. Broad spectrum ALAN could therefore have impacts on the
330 structure of polymorphic populations similar those seen on the peppered moth (*Biston*
331 *betularia*) in the UK during the early 20th century (Cook 2003). This would lead to
332 greater homogeneity in polymorphic populations affected by broad spectrum ALAN,
333 where more conspicuous colourations have been extirpated through enhanced
334 predation or forced to migrate to habitats better suited for crypsis. Similar trends have
335 been documented in a variety of species in response to habitat changes brought on by
336 climate change (Roulin 2014; Delhey & Peters 2017; Jones *et al.* 2020). This may also
337 have a deleterious effect on species that exhibit garish colouration for sexual display at
338 the expense of crypsis (Keren-Rotem *et al.*, 2016), further exacerbating population
339 decline by increasing the predation risk of viable mates.

340 In all predators studied, a shift from LPS to broader light types (HPS, LED, MH)
341 increased the ability to perceive prey. This is likely because the broader spectral
342 composition stimulates the multiple photoreceptors of predators (Davies *et al.*, 2013),
343 enhancing colour discrimination through visual opponent mechanisms that rely on the
344 differences between receptor signals (Vorobyev & Brandt, 1997; Cournoyer & Cohen,
345 2011). While each of the broad light sources provoked a largely similar response in
346 most cases, some notable differences were found between predator responses under
347 different lighting technologies. It is likely that these differences would be more prominent
348 if a broader selection of predator species were studied, given the diverse range of
349 photoreceptor sensitivities that can be exhibited. For instance, visually guided
350 behaviours in predators with spectral sensitivities that extend further into shorter UV
351 wavelengths such as lizards, arachnids and reptiles will likely be most affected by MH
352 technologies that can emit light in the UV range (Davies *et al.*, 2013). The short
353 wavelength, blue peak in LED lighting will also be more likely than other light types to
354 affect marine organisms as it can penetrate further into the ocean (Davies *et al.*, 2014).

355 The impact of broad spectrum lighting on conspicuousness is also variable between
356 receivers. When viewed by the common blenny for example, the relative
357 conspicuousness of yellow colour morphs was not as impacted by broad spectrum
358 lighting compared to the herring gull and shore crab. This is likely because the

359 photoreceptors of the common blenny are more tightly clustered and centred on the
360 green portion of spectrum (Figure 1E). When attempting to interpolate the real-world
361 outcomes of visual models, multiple predators, and their relative impacts on prey
362 populations need to be accounted for.

363 The potential ecological repercussions that arise from the proliferation of modern broad
364 spectrum lighting have been discussed at length (Gaston et al., 2012; Davies et al.,
365 2013; Davies & Smyth, 2018), many of which arise from the facilitation of visually
366 guided behaviours previously limited to the day (Davies et al., 2013). A variety of
367 mitigation methods are available for planners and environmental managers when
368 considering the ecological impacts of ALAN. These include reducing the amount of light
369 used, shielding lights to prevent spill into the surrounding environment, part night
370 lighting during times of peak demand, and manipulating the spectra of lighting to
371 minimise ecological impacts (Gaston *et al.* 2012). Given that broad spectrum facilitates
372 colour discrimination by predators and consequently increases the conspicuousness of
373 prey, it is intuitive to suggest using narrow spectrum lighting to avoid these impacts. In
374 the absence of colour however, nocturnal predators will use luminance contrast
375 perception. We suggest a review of the colour vision systems of nocturnal predators in a
376 given ecosystem should be undertaken to identify those wavelengths of light that
377 minimise luminance contrast perception of prey items against backgrounds. Managers
378 should remain aware however, that the impacts of ALAN extend beyond those on
379 camouflage to impact all aspects of organism biology, and that all parts of the visual
380 spectrum will likely have some ecological impact (Davies & Smyth 2018).

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

387

388 Author Contributions

389 O.M and T.W.D designed the study. O.M conducted the visual modelling, analysis and
390 wrote the first draft of the manuscript. T.W.D carried out the fieldwork and provided
391 guidance throughout the experiment. T.W.D provided irradiance data gathered from his
392 2013 study. T.S. implemented the optical model of light attenuation in seawater. All
393 authors contributed to revisions.

394 Acknowledgements

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

397 Data Availability Statement

398 The data supporting these findings is available via the Dryad Digital Repository
399 <https://doi.org/10.5061/dryad.5hqbzkh7h> (McMahon, Smyth & Davies, 2022).

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589 **Table 1:** The λ_{max} values used to model the spectral sensitivities of the herring gull,
 590 common blenny and green shore crab.

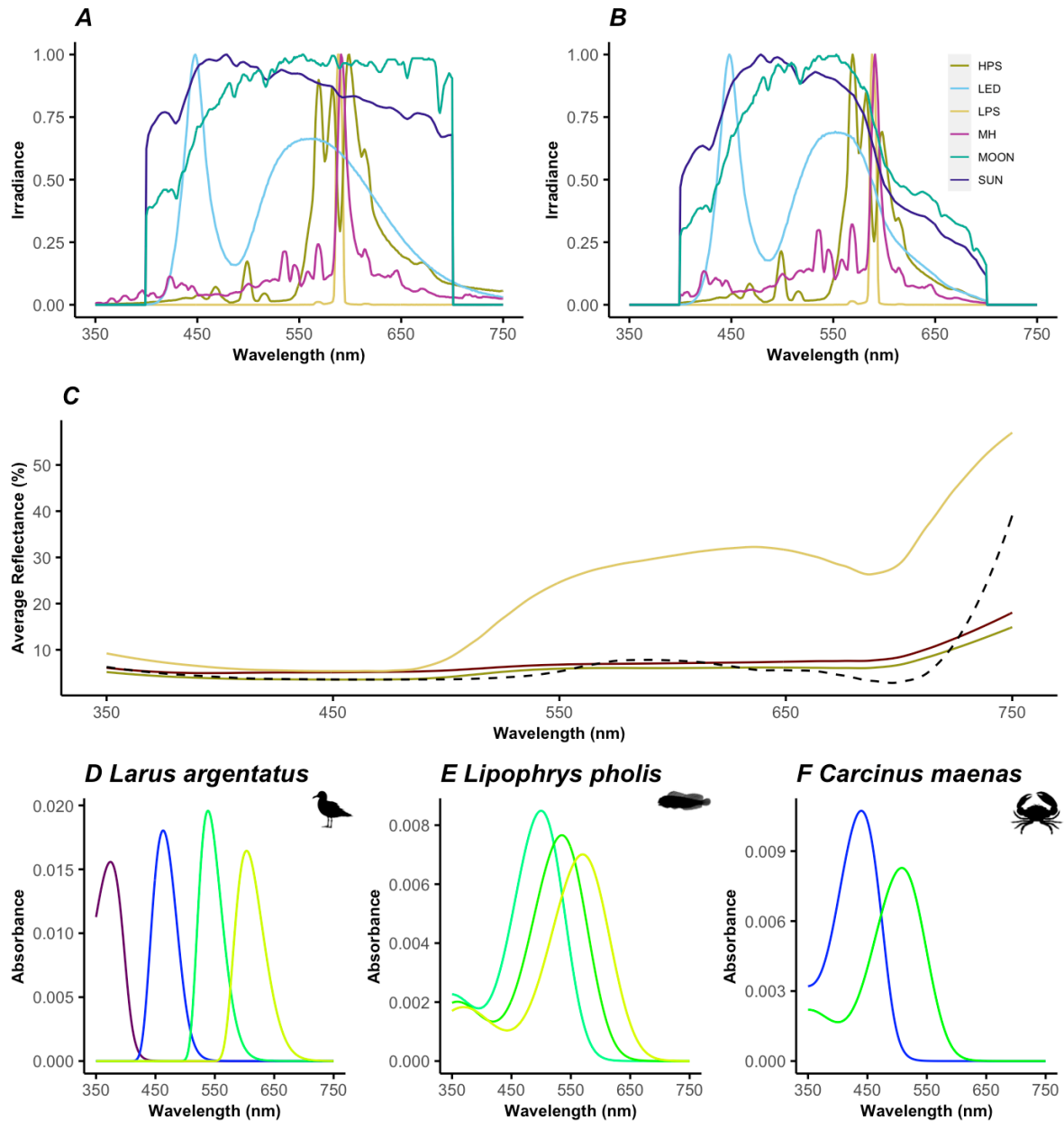
Predator	λ_{max} (nm)	Source
Herring Gull	371, 447, 503, 568	(Crescitelli, 1958; Liebman, cited in Hart, 2001; Hart, 2001; Ödeen & Håstad, 2003)
Common Blenny	500, 535, 570	(Loew & Lythgoe, 1978)
Green Shore Crab	440, 508	(Martin & Mote, 1982)

591

592 **Table 2.** The impact of contrasting lighting **sources** on the comparative
 593 conspicuousness of yellow (Y), Brown (B) and Olive (O) colour morphs of intertidal
 594 littorinid snail (*L. obtusata/L. fabalis*) to three predators with contrasting visual systems
 595 that hunt in air or water. Summarised from Supplementary Tables 3-6.

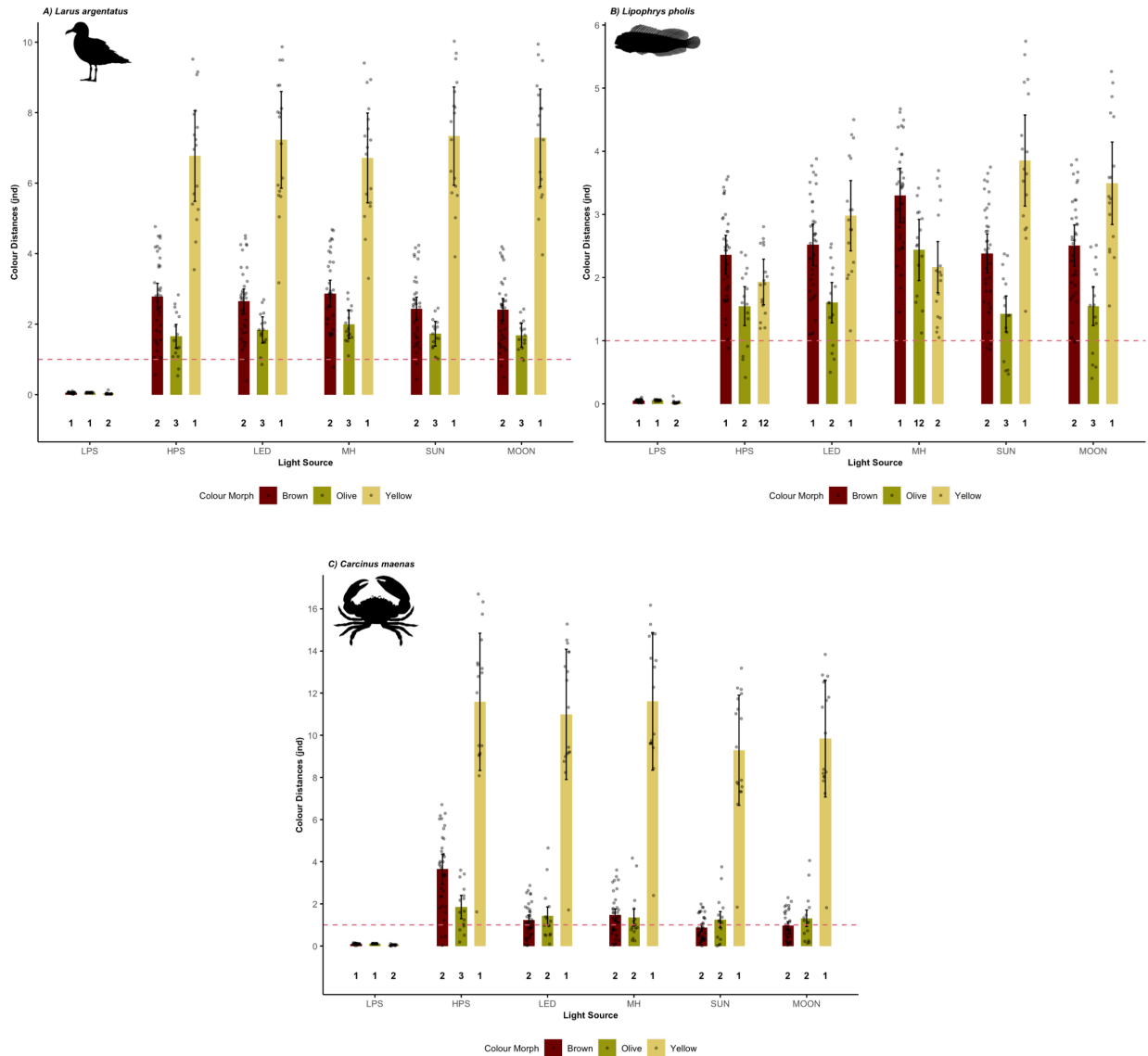
	Herring Gull	Common Blenny	Shore Crab
Visual system	Tetrachromatic	Trichromatic	Dichromatic
Medium	Air	Water	Water
HPS	Y>B>O	Y=B>O; O=Y	Y>B>O
LED	Y>B>O	Y=B>O	Y>B=O
LPS	Y<B=O	Y<B=O	Y<B=O; O=Y
MH	Y>B=O	Y <B=O	Y>B=O
SUN	Y>B=O	Y>B>O	Y>B=O
MOON	Y>B=O	Y=B>O	Y>B=O

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



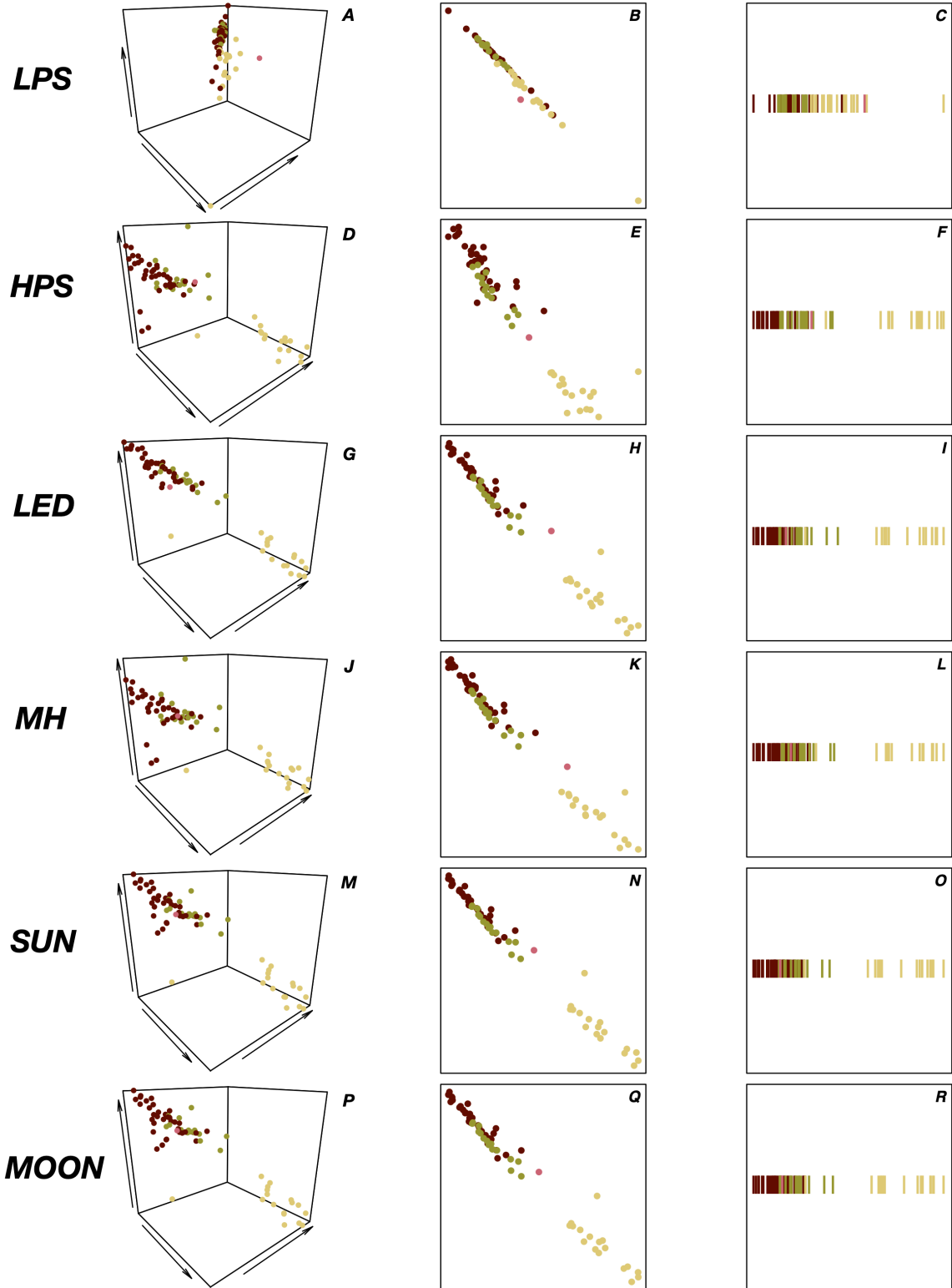
599

600 **Figure 1. Spectra used to parametrize visual modelling of the conspicuous of**
 601 **littorinid snail colour morphs to three visual predators. A. In air relative**
 602 **irradiances used in models for the Herring Gull (*L. argentatus*). Irradiances have**
 603 **been scaled to between 0 and 1 to facilitate comparison of contrasting spectral**
 604 **compositions. B. Model in water relative irradiances (3m depth) used to**
 605 **parametrize models for the common blenny (*L. pholis*) and shore crab (*C.***
 606 ***maenas*). C. Averaged reflectance spectrum collected from yellow, olive and brown**
 607 **morphs of *L. obtusata* and *L. fabalis*. The averaged reflectance spectrum for the fucoid**
 608 **algae background is given as a dashed black line. D-F. The modelled spectral**
 609 **absorbance curves of the photoreceptors in the eyes of each visual predator.**



610

611 **Figure 2: The impact of four alternative lighting technologies on the conspicuousness of**
 612 **three different colour morphs of intertidal littorinid snail to three predators with**
 613 **contrasting colour vision systems.** Plot is derived from colour distance data indicating
 614 the chromatic contrast between *Littorina* and its natural background, as viewed by a
 615 predator. Bars represent model mean values, error bars represent 95% confidence
 616 limits. Grey dots represent raw *Littorina* colour distance values. Numbers in bold
 617 indicate significant differences between the effects of each light type at the 95%
 618 confidence level, where numbers differ within each colour morph grouping (see
 619 Supplementary Tables 1-3 for results of pairwise contrasts). **The dashed line indicates**
 620 **1 JND, the minimum threshold of detectability.** Where these numbers are shared
 621 within a colour morph group, no significant difference can be inferred.



623 **Figure 3. The impact of various light sources on the colour distances**
624 **between camouflaged prey and their background by intertidal predators.**
625 Colour distances between yellow, olive and brown colour morphs of *L. obtusata*
626 and *L. fabalis* as perceived by the **tetrachromatic herring gull (*L. argentatus*,**
627 **A,D,G,J,M,P)**, the **trichromatic common blenny (*L. pholis*, B,E,H,K,N,Q)** and
628 **the dichromatic shore crab (*C. maenas*, C,F,I,L,O,R)** under **Low Pressure**
629 **Sodium (A-C), High Pressure Sodium (D-F), LED (G-I), MH (J-L) outdoor**
630 **lighting technologies. Colour distances between different morphs**
631 **illuminated by the Sun (M,N,O) and Moon (P,Q,R) are also provided. Red**
632 **points represent the fucoid algae background.**