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Artificial light at night alters predation on colour-polymorphic camouflaged prey

Emma Moyses^{a*}, Dr Louise B. Firth^a, Dr Tim Smyth^b, Dr Svenja Tidau^a, Dr Thomas W. Davies^a

^aSchool of Biological and Marine Sciences, University of Plymouth, Plymouth PL4 8AA, UK

^bPlymouth Marine Laboratory, Prospect Place, Plymouth PL1 3DH, UK

*Corresponding author: emma.moyses@postgrad.plymouth.ac.uk

Abstract

Artificial light at night (ALAN) disrupts biological processes across taxa and at all levels of organisation. Despite growing interest in this globally pervasive sensory pollutant, its impact on colour-guided processes remains largely unexplored. This is especially concerning given the rapid transition in recent years away from narrow-spectrum lighting and towards broad-spectrum options such as white LEDs, which are rich in the short wavelengths of light to which many taxa are particularly sensitive. Camouflage is particularly likely to be disrupted by broader spectra of ALAN due to changes in conspicuousness in background matching prey, which may alter prey recognition in visually guided predators. We simulated natural intensities of moonlight with and without ALAN, using both broad-spectrum ('white') ALAN and ALAN filtered to remove the characteristic short (blue) wavelength peak of broad-spectrum LEDs to test whether filtering might mitigate their effects. We tested how exposure to these light treatments impacted predator-prey interactions, using the intertidal crab *Carcinus maenas* and contrasting colour morphs of the colour-polymorphic snail *Littorina obtusata* as a model system. Exposure to broad-spectrum ALAN reduced overall predation and reversed the pattern of colour-based prey selection observed under control conditions. Snails

were 55% less likely to be attacked under broad-spectrum ALAN than in control conditions, with likelihood decreasing over 70% for yellow snails. Yellow snails were over 26% more likely to be attacked than brown ones under control conditions, but brown snails were over 40% more likely to be attacked than yellow ones under broad-spectrum ALAN. Exposure to filtered ALAN removed any significant colour-based difference in prey recognition. Our results demonstrate that spectral composition is a crucial aspect of ALAN as a sensory pollutant, capable of instigating profound changes in predator-prey interactions that could drive changes in population demography and increase morphological homogeneity in species that depend on colour polymorphism for camouflage.

Keywords: Artificial light at night; artificial light spectra; light pollution; camouflage; colour polymorphism; visual ecology; global change; species interactions; invertebrate

Introduction

Artificial light at night (ALAN) is one of the most important but least well understood sensory pollutants. It is globally prevalent (Falchi *et al.* 2016) and growing (Kyba *et al.* 2017), with well-documented biological impacts across taxa, spatial scales, and levels of biological organisation from the cellular to ecosystem processes (Knop *et al.* 2017, Davies and Smyth 2018; Sanders *et al.* 2021). ALAN affects at least 23% of Earth's land surface between 75°N and 60°S and 80% of the global human population (Falchi *et al.* 2016), expanding in area by 2.2% and in intensity by 1.8% annually (Kyba *et al.* 2017). The use of broad-spectrum LEDs, which utilise wavelengths across the entire visible spectrum and are often described as producing 'white' light (Pimputkar *et al.* 2009), has increased in recent decades, expanding from 9% to 45% of the lighting market in just three years between 2011 and 2014 (Zissis & Bertoldi 2014), and projected to make up 85% of street lighting worldwide by 2028 (Northeast Group LLC 2019). This rapid shift from traditional narrow-spectrum lighting to broad-spectrum technologies (Kyba *et al.* 2017) means that ever more species are exposed to and able to detect ALAN (Davies *et al.* 2013; Pawson & Bader 2014). LEDs have two

characteristics which make them potentially more harmful to the environment than traditional lighting: first, their short wavelength peak (at around 450 nm, which appears blue to human eyes) coincides with the wavelengths to which many taxa are particularly sensitive, meaning LEDs have the potential to affect more species than any other form of lighting (Pawson & Bader 2014), particularly in the marine environment, where blue light penetrates deeper into the water column than other wavelengths (Tamir *et al.* 2017; Tidau *et al.*, 2021). Second, the broader range of wavelengths emitted means that ALAN from LEDs is likely to affect a larger number of species (Gaston *et al.* 2012). One of the most overlooked mechanisms by which ALAN modifies the environment in the 21st century is the disruption of colour-guided behaviours such as foraging, intra-species communication, and camouflage in a way that has previously not been possible (Davies *et al.* 2013).

Camouflage is one of the key methods through which prey species evade predation by visually guided predators. Background-matching, arguably the most common form of camouflage (Caro & Koneru 2020), may be especially vulnerable to disruption from changes in illumination (Endler 1993). Background matching works when an organism's colouration appears, from a predator's perspective, to closely match that of its habitat (Cott 1940; Thayer 1909). It is particularly common in small, relatively sessile organisms, with clear associations between colouration and expected lighting conditions (Caro *et al.* 2012). For example, diurnal mammals often exhibit spotted coats that resemble dappled sunlight (Caro & Koneru 2020). Habitats are rarely homogenous and so many species exhibit colour polymorphism, with individuals of several different colours existing within a population, allowing at least some individuals to background match at different times or locations in complex habitats (Duarte *et al.* 2018). Maintenance of multiple colourmorphs is complex (Karpestam *et al.* 2016) but has been shown to benefit cryptic individuals when selective predation occurs (Johannesson & Ekendahl 2002; Karpestam *et al.* 2016) and to disrupt search image formation (i.e., the ability to rapidly recognise frequently encountered prey) in predators (Troscianko *et al.* 2021). This occurs commonly in spatially and temporally complex environments such as intertidal coastal habitats, where both visual predators and colour-polymorphic prey species are widespread. The

correlation between visual complexity of the environment and variation in animal colouration has been demonstrated in shore crabs, for example, which exhibit more variable colouration in rockpools than on mudflats, where their colour is more uniform (Nokelainen *et al.* 2017).

If camouflage is disrupted by ALAN, the ecological impacts could be profound. Preliminary evidence from modelling studies suggests that ALAN spectral shifts affect the conspicuousness of camouflaged prey (Briolat *et al.* 2021; McMahon *et al.* 2022). If these impacts translate into real-world changes to prey selection by predators, predator-prey interactions may be unbalanced, causing changes in population demography as colour ratios in polymorphic prey are altered and selection pressure shifts. These knock-on effects of camouflage disruption have been clearly demonstrated by Kettlewell's now classic investigations into the peppered moth *Biston betularia*, which showed that pollution in the form of black soot on tree trunks made light-coloured individuals (*typica*) more visible to their avian predators, whereas brown-coloured individuals (*carbonaria*) remained camouflaged and so were less vulnerable to predation, quickly becoming the overwhelmingly dominant morph in polluted areas (Kettlewell 1955, 1956, 1958). Such a process instigated by spectral changes in ALAN could ultimately result in changes to the genetic structure of affected populations (McMahon *et al.* 2022). However, it is important to note that visual modelling studies are unable to account for behavioural factors beyond the purely mechanistic, and so their conclusions must be tested in a practical setting in order to expand our understanding of these complex interactions. Clearly, research into this aspect of ALAN is urgently required.

Using a custom-built experimental system capable of accurately simulating real-time natural lighting conditions in a laboratory setting (Tidau *et al.* 2022), we investigated the impact of different ALAN spectra on predation of a colour-polymorphic snail (*Littorina obtusata*) on a simulated fucoid macroalgae background by an intertidal predator (*Carcinus maenas*). The experimental set up enabled us to practically test hypotheses that were derived from a previous modelling study (McMahon *et al.* 2022). We tested whether the presence of broad-spectrum ALAN and/or ALAN with

a filter to remove blue wavelength spectra altered the predation rates and colour-based prey recognition by *C. maenas* observed under simulated natural night-time light conditions. We predicted that broad-spectrum ALAN would increase conspicuousness of different colour morphs, and therefore increase their susceptibility to predation, in comparison to filtered ALAN. Based on the visual modelling of McMahon *et al.* (2022), we hypothesised that yellow morphs would be more conspicuous and therefore experience higher predation rates than brown morphs under broad spectrum ALAN, and that there would be no difference in predation rates between morphs under filtered ALAN.

Materials and Methods

Study species

The flat periwinkle, *Littorina obtusata*, is a widely distributed marine gastropod common on UK shores. It is usually found on fucoid macroalgae (*Fucus serratus*, *Fucus vesiculosus*, and *Ascophyllum nodosum*), upon which it grazes and against which it is believed to appear camouflaged to predators (Wilbur & Steneck 1999; Johannesson & Ekdahl 2002; Crothers 2012). It exhibits extensive colour polymorphism, with yellow and brown morphs being the most common, but other colours such as green, orange, and white as well as striped and tessellated patterns also occurring (Johannesson & Ekdahl 2002). It has been proposed that this variation in colour closely matches that of its algal substrate (Reimchen 1979; Wilbur & Steneck 1999). The green shore crab, *Carcinus maenas*, is one of *L. obtusata*'s main predators and selective predation by this species is known to directly affect the snail's demography and population density (Pettitt 1975; Reimchen 1979; Williams 1992), even prompting rapid changes in snail morphology following its arrival as an invasive species in North America (Seeley 1986). *C. maenas* predominantly feeds nocturnally (Ropes 1968; Baeta *et al.* 2006). While it utilises several methods to detect prey, including chemosensing, (Shelton & Mackie 1971; Robinson *et al.* 2011) and random tactile searches (Crothers 1968b; Elnor & Hughes 1978), it is also a

visual predator, reacting particularly strongly to movement and contrast (Crothers 1968a; Pettitt 1975). While some uncertainty about the precise visual capabilities of *C. maenas* remains, they are believed to be dichromats like other brachyurans (Martin & Mote, 1982; Cronin & Hariyama 2002), with some ability to distinguish between colours. However, it should be noted that even if their vision were not dichromatic but rather monochromatic, they would still be able to perceive differences in brightness (luminance) between coloured objects with markedly different luminance (Ekendahl 1998), such as the yellow and brown shells used here.

Experimental setup

Live *Carcinus maenas* (hereafter *Carcinus*) (n = 65) and *Littorina obtusata* (hereafter *Littorina*) (n = 1200) were collected from the rocky shore at Mountbatten, Plymouth, UK (50.3755° N, 4.1427° W) between 22 August and 16 September 2022 and transported separately to the University of Plymouth. *Carcinus* were collected 48 hours prior to observations throughout the experimental period to prevent tank acclimation and to ensure sampling across the different phases of the lunar cycle (Tidau *et al.* 2022) and were starved during this period between collection and observations. We selected healthy adult crabs and excluded animals that were visibly injured or parasitised, soft-shelled (recently moulted), berried females, and juveniles with shell width <30 mm at the widest point. *Littorina* were visually inspected for shell damage; undamaged yellow-shelled ('yellow') and brown-shelled ('brown') individuals measuring 4-10 mm at the widest shell point were retained as prey.

Animals were randomly assigned to one of three light treatments: natural light regime ('control night', crabs: n = 15, 10 x female, 5 x male, mean shell width = 40.93 mm ± 5.88 mm [SE]), moonlight + 10 lx cool white LED (broad-spectrum) ALAN ('ALAN', crabs: n = 15, 9 x female, 6 x male, mean shell width = 39.8 mm ± 4.81 mm [SE]), moonlight + 10 lx cool white LED ALAN with blue wavelengths <510 nm filtered out to test the potential for mitigating broad-spectrum ALAN ('mitigation', crabs: n

= 15, 9 x female, 6 x male, mean shell width = 38.1 mm \pm 3.75 mm [SE]). There was no significant difference in crab size between treatments ($F_{2,42} = 0.378$, $p = 0.688$). The ALAN treatment intensity of 10 lx was selected as it is conservatively comparable to levels measured at the water's surface on light-polluted UK shores (e.g., Davies *et al.* 2015). Treatments ran concurrently on a total of 15 nights (total crabs $n = 45$). Each light treatment chamber contained one 24 l clear Perspex tank (38 \times 23 \times 27 cm) half-filled with filtered seawater, which was changed between observations (one replicate per chamber). Each tank housed one crab which was provided with 10 x yellow *Littorina* and 10 x brown *Littorina* simultaneously. Individual crabs were used for one replicate of one treatment only and were not reused for additional treatments or replicates to avoid any influence of prior treatment exposure on subsequent replicates. To simulate natural background camouflage conditions, the tanks' internal surfaces were covered with laminated printed photographs of *Fucus vesiculosus* taken at the collection site at the start of the experimental period. Treatment chambers were light-sealed with two layers of blackout fabric sealed around the edges of the chamber with Velcro tape to prevent ambient light from entering the experimental setup and to ensure different light treatments did not influence each other.

Natural light conditions were simulated as experienced at the collection site following Tidau *et al.* (2022). Daylight was simulated using AquaRay Natural Daylight Tiles set at 5000 lx (mean 4781 lx \pm 5%) and a BioLumen Control Unit (Tropical Marine Centre UK) programmed to the real time sunrise and sunset times in Plymouth, UK (50.3755° N, 4.1427° W). Tiles were covered with 3mm frosted Perspex to ensure even light diffusion and minimisation of bright spots (Tidau *et al.* 2021). Moonlight conditions were simulated using 'artificial moons' consisting of diffusing spheres each containing a bank of 2700-3500 K 1.2 cd LEDs; a pulse width modulated signal (scale 0-100%) applied to the 5 V output of a Raspberry Pi 3 model B+ simulated natural moonlight conditions (maximum lunar brightness 0.5 lx). For light treatment spectra, see Tidau *et al.* 2022, supplementary material S2; for a photograph of the experimental light setup, see Tidau *et al.* 2021. Lunar brightness was adjusted from a 1-minute resolution look up table of Zenith Sky Brightness modelled for Plymouth: the time,

date, and geocentric coordinates of location were used to calculate the moon's sky position and phase angle (CRAN: astrolib, Chakraborty *et al.* 2014) (Davies *et al.* 2013), allowing Zenith Sky Brightness to be modelled taking lunar phase, altitude, opposition, parallax, and atmospheric scattering into account following Krisciunas and Schaefer (1991). This system allows us to accurately simulate variations in nocturnal light intensity and timing as the moon crosses the sky (Tidau *et al.* 2022) while retaining greater control over other environmental variables than would be possible in the field, enabling us to assess the impacts of ALAN specifically more confidently, although the accurate simulation of natural spectral changes, particularly tidally driven ones, remains unresolved (Tidau *et al.* 2021).

ALAN was simulated in two chambers between dusk and dawn for the time of year at Plymouth, UK, using AquaRay cool white FlexiLED strips (Tropical Marine Centre, UK) triggered by a CellOptick 12 V photocell; brightness was controlled via voltage dimming. The mitigation treatment was created in one of these chambers by minimising the LEDs' blue wavelengths using a long bandpass (510-2200 nm) yellow acrylic filter (Knight Optical (UK) Ltd).

Animals were exposed to experimental conditions undisturbed between dusk and dawn, after which damage to the *Littorina* was assessed. *Littorina* were classed as having been 'attacked' if the shell was crushed, intact but empty, or if it had been visibly damaged. Live snails in undamaged shells were classed as 'not attacked'.

Analysis

Statistical analysis was carried out using R (RStudio version 2022.07.2+576; R Core Team, 2022). Snails' probability of being attacked (binary: attacked/not attacked) was quantified using mixed effects logistic regression modelling. To test hypotheses relating to differences between night lighting treatments, a binomial generalised linear mixed-effects model (GLMM) was fitted with the interaction between light treatment (control night, ALAN, mitigation) and shell colour (brown, yellow) as the independent variable. Replicate ('crab') was included as a random variable to control

for repeated behavioural observations: $\text{outcome} \sim \text{treatment} * \text{colour} + (1 | \text{crab})$ (CRAN: lme4, Bates *et al.* 2009). Impacts of treatment and colour were investigated using type II Wald Chi-square tests (CRAN: car, Fox *et al.* 2012). Significant differences between treatment levels and shell colours and between treatment levels and overall attack probability were investigated using post-hoc pairwise comparisons via the contrast function (CRAN: emmeans, Lenth *et al.* 2019). The p-values were adjusted using the FDR method to control for Type I errors.

Results

A total of 374 snails (191 yellow, 183 brown) were attacked. Exposure to broad-spectrum ALAN reduced snails' overall attack likelihood by 55% compared to control night conditions (estimated marginal mean probabilities: control night = 0.540, ALAN = 0.243) (see **Table 3**). Yellow snails were over 26% more likely to be attacked than brown ones under natural night-time light conditions (estimated marginal mean probabilities: yellow = 0.623, brown = 0.456), but under broad-spectrum ALAN this pattern was reversed, with brown snails over 40% more likely to be attacked than yellow ones (estimated marginal mean probabilities: yellow = 0.181, brown = 0.306) (see **Table 2**); under the mitigation treatment there was no difference in the likelihood of being attacked between shell colours (see *figure 1* and **Table 2**). Probability of attack was influenced by treatment ($\chi^2 = 6.97$, $d. = 2$, $p = 0.03$), and there was a significant interaction between treatment and shell colour ($\chi^2 = 12.79$, $d. = 2$, $p = 0.002$; see **Table 1**). Broad-spectrum ALAN reduced the likelihood of yellow snails being attacked by over 70% relative to natural night-time light conditions (estimated marginal mean probabilities: ALAN = 0.181, control night = 0.623; *figure 1*). Mitigated ALAN did not reduce the likelihood of snails of either colour morph being attacked compared to control night-time conditions (see **Table 3**).

Discussion

ALAN is known to increase predation pressure on a variety of prey species (Bennie *et al.* 2018; Bolton *et al.* 2017; Underwood *et al.* 2017). Modelling studies suggest that disrupted background-matching camouflage may be an explanatory mechanism (Briolat *et al.* 2021; McMahon *et al.* 2022). We tested this experimentally. Our results support this conclusion and demonstrate that the spectral makeup of ALAN plays a key role in predation. Broad-spectrum ALAN reduced overall predation, but mitigated ALAN did not, while both ALAN types altered the predators' colour-based prey selection: yellow colour morphs were more likely to be preyed upon under control conditions than brown morphs, but this pattern was reversed under broad-spectrum ALAN, while mitigated ALAN seemingly eliminated colour-based selection altogether.

Contrary to our expectations, and despite modelling predicting their increased conspicuousness, predation on yellow morphs was reduced under broad-spectrum ALAN both in overall terms and when compared to brown morphs under the same lighting conditions. It should be noted, however, that in the absence of an ability to accurately detect colour (such as in monochromats, or in dim moonlight), visually guided predators are likely to resort to luminance contrast perception, assessing the 'lightness' or 'darkness' of an object rather than its specific colour (Nokelainen *et al.* 2021). This may explain the higher predation rates on yellow morphs observed under control night conditions, since they are likely to appear brighter (in terms of luminance) than brown morphs against a relatively dark, unilluminated background. Furthermore, these unexpected results indicate that simple conspicuousness of prey as determined by background colour-matching is unlikely to be the sole determinant of predators' hunting behaviour, highlighting the importance of testing modelling-derived predictions in practical settings. Further behavioural research is needed to explore additional factors that may influence behaviour, such as stress responses to artificial light, measures of interindividual variability such as boldness, and potential acclimation to ALAN.

Carcinus mainly hunts nocturnally (Crothers 1968a; Ropes 1968; Rangeley and Thomas 1987; Baeta et al. 2006), meaning that it may face additional complications resulting from changes to the ability to carry out visually guided processes at night. Our finding that *Carcinus* hunted significantly less under broad-spectrum ALAN (but not under mitigated ALAN) suggests that broad-spectrum light pollution may act similarly to sunlight in inhibiting *Carcinus*' ability or willingness to hunt, in a sense extending "day" into the nocturnal environment. Indeed, it has been suggested that ALAN, and especially broad-spectrum ALAN, may also enable diurnal species to carry out colour-guided behaviours such as selective predation at night (Davies *et al.* 2013). This may bring nocturnal species into direct competition with diurnal ones in a way that has previously not been possible, for example in plant-pollinator networks (MacGregor *et al.* 2015). Any such shifts are likely to further complicate interactions in our model system, since *Littorina* has several diurnal predators (mainly fish and birds) which also prey on *Carcinus*. Therefore, to ensure a more complete assessment of the impact of ALAN on predator-prey interactions, multiple predator species with a variety of lifestyles should be considered, both individually and in combination with each other.

The reversal of *Carcinus*' pattern of prey selection by broad-spectrum ALAN may have significant ecological implications. Environmental changes that disrupt the effectiveness of camouflage, such as coral bleaching or visible pollution residue, have been shown to impact the fitness of camouflage-dependent species (Coker *et al.* 2009; Kettlewell 1956, 1958), which can in turn translate into dramatic changes in population structure for colour polymorphic species (Kettlewell 1958; Cook 2003). While previous studies have focused on physical substrate changes (Kettlewell 1955; Cook 2003; Coker *et al.* 2009), it is reasonable to assume that light, a fundamental aspect of the visual processes that enable colour vision and by extension, camouflage, is similarly capable of instigating such changes. As a result, we might expect broad-spectrum ALAN exposure to result in increasingly homogenous phenotypes in colour polymorphic species, ultimately reducing the genetic diversity of exposed populations.

Several mitigation methods are available to reduce the ecological impact of ALAN, including reducing overall light intensity and quantity, shielding or directing lights to limit their area of impact, and, as has been frequently recommended in the ecological literature, tailoring ALAN spectra to reduce biological impacts (Gaston *et al.* 2012; Longcore *et al.* 2015; Spoelstra *et al.* 2015; Davies & Smyth 2018). This latter option may seem especially effective in light of our findings that filtered ALAN did not result in the same reversal of colour-based prey selection observed under broad-spectrum ALAN. However, although there is some evidence to suggest that longer wavelengths (from filtered yellow-green and amber LEDs) are likely to have the smallest impacts on many organisms (Longcore *et al.* 2018), it is important to note that, given the broad range of wavelengths biological processes have evolved to utilise, it is extremely unlikely that any one spectrum will result in no ecological impact at all (Davies & Smyth 2018). Similarly, while our results may suggest that older, narrow-spectrum lighting technologies were probably less disruptive to camouflage, the benefits of LEDs cannot be dismissed out of hand. Perhaps somewhat ironically, one of the major drivers of their rapid uptake has been their perceived 'greenness' due to their energy efficiency and subsequently lower carbon emissions compared to older lighting technologies. Clearly, balancing these concerns must be an urgent focus for planners and managers as our understanding of the impacts of different lighting technologies continues to develop.

This study has demonstrated that broad-spectrum artificial light at night can have a profound impact on predator-prey interactions by changing the visual environment, altering predation patterns on a polymorphic prey species. By testing modelling-derived hypotheses in a behavioural context, we have provided insight into the complex interactions between theoretical prey conspicuousness and real-world predation behaviour. If increasingly widespread broad-spectrum LED technologies continue to alter predation patterns in the long term, the selective predation of specific colour morphs is likely to become increasingly important, potentially altering the population demography of colour-polymorphic species, which are widespread across taxa and ecosystems, both marine and terrestrial. Ultimately, our results indicate that broad-spectrum ALAN is likely to increase

morphological homogeneity, further compounding existing issues of physical and structural homogenisation caused by urbanisation, which in turn result in biotic and functional homogenisation via reductions in species diversity and erosion of ecosystem functioning (see Firth *et al.* 2016). Since urbanisation is itself the main vehicle for ALAN's expansion worldwide (Falchi *et al.* 2016; Kyba *et al.* 2017), it is clear that these two drivers of homogeneity are intricately linked. As the human population increases and urban areas continue to expand, a holistic approach to assessing and managing human impacts on the environment will be needed, and must include consideration not only of physical changes, but also of sensory pollutants such as ALAN and its changing spectra.

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References

- Baeta, A., Cabral, H. N., Marques, J. C., & Pardal, M. A. (2006). Feeding ecology of the green crab, *Carcinus maenas* (L., 1758) in a temperate estuary, Portugal. *Crustaceana*, 1181-1193.
- Caro, T., & Koneru, M. (2021). Towards an ecology of protective coloration. *Biological Reviews*, 96(2), 611-641.
- Caro, T., Stankowich, T., Mesnick, S. L., Costa, D. P., & Beeman, K. (2012). Pelage coloration in pinnipeds: functional considerations. *Behavioral Ecology*, 23(4), 765-774.
- Chakraborty, A., Feigelson, E., & Babu, G. (2014). astrolabe: Astronomy Users Library for R. URL: <http://CRAN.R-project.org/package=astrolibR>.
- 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(6), 1204-1210.
- Cook, L. M. (2003). The rise and fall of the *carbonaria* form of the peppered moth. *The Quarterly Review of Biology*, 78(4), 399-417.
- Cott, H. B. (1940). *Adaptive coloration in animals*. Methuen & Co., Ltd.
- Cronin, T. W., & Hariyama, T. (2002). Spectral sensitivity in crustacean eyes. *The crustacean nervous system*, 499-511.
- Crothers, J. (1968)a. The biology of the shore crab *Carcinus maenas* (L.) 1. The background-anatomy, growth and life history. *Field studies*, 2(4), 407-434.
- Crothers, J. (1968)b. The biology of the shore crab, *Carcinus maenas* (L.). 2. The life of the adult crab. *Field Studies*, 2, 579-614.
- Crothers, J. (2012). *Snails on rocky sea shores* (Vol. 30). 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(5), 1417-1423.

- Davies, T. W., Coleman, M., Griffith, K. M., & Jenkins, S. R. (2015). Night-time lighting alters the composition of marine epifaunal communities. *Biology Letters*, *11*(4), 20150080.
<https://doi.org/doi:10.1098/rsbl.2015.0080>
- 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*(3), 872-882.
- 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*(1), 1-10.
- Ekendahl, A. (1998). Colour polymorphic prey (*Littorina saxatilis Olivi*) and predatory effects of a crab population (*Carcinus maenas* L.). *Journal of Experimental Marine Biology and Ecology*, *222*(1), 239-246. [https://doi.org/https://doi.org/10.1016/S0022-0981\(97\)00147-0](https://doi.org/https://doi.org/10.1016/S0022-0981(97)00147-0)
- Elnor, R. W., & Hughes, R. N. (1978). Energy Maximization in the Diet of the Shore Crab, *Carcinus maenas*. *Journal of Animal Ecology*, *47*(1), 103-116. <https://doi.org/10.2307/3925>
- Endler, J. A. (1993). The color of light in forests and its implications. *Ecological monographs*, *63*(1), 1-27.
- 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*(6), e1600377. <https://doi.org/doi:10.1126/sciadv.1600377>
- Firth, L. B., Knights, A. M., Bridger, D., Evans, A. J., Mieszkowska, N., Moore, P. J., O'Connor, N. E., Sheehan, E. V., Thompson, R. C., & Hawkins, S. J. (2016). Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanography and Marine Biology: an annual review*, *54*, 189-262.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., & Graves, S. (2012). Package 'car'. *Vienna: R Foundation for Statistical Computing*, 16.
- 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*(6), 1256-1266.

- Johannesson, K., & Ekendahl, A. (2002). Selective predation favouring cryptic individuals of marine snails (*Littorina*). *biological Journal of the Linnean Society*, *76*(1), 137-144.
- Karpestam, E., Merilaita, S., & Forsman, A. (2016). Colour polymorphism protects prey individuals and populations against predation. *Scientific Reports*, *6*(1), 1-10.
- Kettlewell, H. B. D. (1955). Recognition of Appropriate Backgrounds by the Pale and Black Phases of Lepidoptera. *Nature*, *175*(4465), 943-944. <https://doi.org/10.1038/175943a0>
- Kettlewell, H. B. D. (1956). Further selection experiments on industrial melanism in the Lepidoptera. *Heredity*, *10*(3), 287-301. <https://doi.org/10.1038/hdy.1956.28>
- Kettlewell, H. B. D. (1958). A survey of the frequencies of *Biston betularia* (L.) (Lep.) and its melanic forms in Great Britain. *Heredity*, *12*(1), 51-72. <https://doi.org/10.1038/hdy.1958.4>
- Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature*, *548*(7666), 206-209. <https://doi.org/10.1038/nature23288>
- Krisciunas, K., & Schaefer, B. E. (1991). A model of the brightness of moonlight. *Publications of the Astronomical Society of the Pacific*, *103*(667), 1033.
- 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*(11), e1701528. <https://doi.org/doi:10.1126/sciadv.1701528>
- Length, 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>
- Longcore, T., Aldern, H. L., Eggers, J. F., Flores, S., Franco, L., Hirshfield-Yamanishi, E., Petrinec, L. N., Yan, W. A., & Barroso, A. M. (2015). Tuning the white light spectrum of light emitting diode lamps to reduce attraction of nocturnal arthropods. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1667), 20140125. <https://doi.org/doi:10.1098/rstb.2014.0125>

- Longcore, T., Rodríguez, A., Witherington, B., Penniman, J. F., Herf, L., & Herf, M. (2018). Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*, 329(8-9), 511-521.
- Macgregor, C. J., Pocock, M. J. O., Fox, R., & Evans, D. M. (2015). Pollination by nocturnal Lepidoptera, and the effects of light pollution: a review. *Ecological Entomology*, 40(3), 187-198. <https://doi.org/10.1111/een.12174>
- Martin, F. G., & Mote, M. I. (1982). Color receptors in marine crustaceans: A second spectral class of retinular cell in the compound eyes of *Callinectes* and *Carcinus*. *Journal of comparative physiology*, 145(4), 549-554. <https://doi.org/10.1007/BF00612820>
- McMahon, O., Smyth, T., & Davies, T. W. (2022). Broad spectrum artificial light at night increases the conspicuousness of camouflaged prey. *Journal of Applied Ecology*, 59(5), 1324-1333. <https://doi.org/10.1111/1365-2664.14146>
- Merilaita, S., Scott-Samuel, N. E., & Cuthill, I. C. (2017). How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 372(1724), 20160341. <https://doi.org/10.1098/rstb.2016.0341>
- Nokelainen, O., Hubbard, N., Lown, A. E., Wood, L. E., & Stevens, M. (2017). Through predators' eyes: phenotype–environment associations in shore crab coloration at different spatial scales. *biological Journal of the Linnean Society*, 122(4), 738-751. <https://doi.org/10.1093/biolinnean/blx101>
- Nokelainen, O., de Moraes Rezende, F., Valkonen, J. K., & Mappes, J. (2021). Context-dependent coloration of prey and predator decision making in contrasting light environments. *Behavioral Ecology*, 33(1), 77-86. <https://doi.org/10.1093/beheco/arab111>
- Northeast Group LLC. (2019). *Global smart street lighting & smart cities: Market forecast (2019–2028)* [Technical Report] (4849803).
- Pawson, S. M., & Bader, M.-F. (2014). LED lighting increases the ecological impact of light pollution irrespective of color temperature. *Ecological Applications*, 24(7), 1561-1568.

- Pettitt, C. (1975). A review of the predators of *Littorina*, especially those of *L. saxatilis* (*Olivi*)(Gastropoda: Prosobranchia). *Journal of Conchology*, 28, 343-357.
- Pimputkar, S., Speck, J. S., DenBaars, S. P., & Nakamura, S. (2009). Prospects for LED lighting. *Nature Photonics*, 3(4), 180-182. <https://doi.org/10.1038/nphoton.2009.32>
- R Core Team (2022). *R: A language and environment for statistical computing*. In R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rangeley, R. W., & Thomas, M. L. H. (1987). Predatory behaviour of juvenile shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology*, 108(2), 191-197. [https://doi.org/https://doi.org/10.1016/S0022-0981\(87\)80023-0](https://doi.org/https://doi.org/10.1016/S0022-0981(87)80023-0)
- Reimchen, T. E. (1979). Substratum heterogeneity, crypsis, and colour polymorphism in an intertidal snail (*Littorina maria*e). *Canadian Journal of Zoology*, 57(5), 1070-1085. <https://doi.org/10.1139/z79-135>
- Robinson, E. M., Smee, D. L., & Trussell, G. C. (2011). Green crab (*Carcinus maenas*) foraging efficiency reduced by fast flows. *PLOS ONE*, 6(6), e21025. <https://doi.org/10.1371/journal.pone.0021025>
- Ropes, J. W. (1968). The feeding habits of the green crab, *Carcinus maenas* (L.). *Fishery Bulletin*, 67(2), 183-203.
- Sanders, D., Frago, E., Kehoe, R., Patterson, C., & Gaston, K. J. (2021). A meta-analysis of biological impacts of artificial light at night. *Nature Ecology & Evolution*, 5(1), 74-81.
- Seeley, R. H. (1986). Intense natural selection caused a rapid morphological transition in a living marine snail. *Proceedings of the National Academy of Sciences*, 83(18), 6897-6901.
- Shelton, R. G. J., & Mackie, A. M. (1971). Studies on the chemical preferences of the shore crab, *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology*, 7(1), 41-49. [https://doi.org/https://doi.org/10.1016/0022-0981\(71\)90003-7](https://doi.org/https://doi.org/10.1016/0022-0981(71)90003-7)
- Spoelstra, K., van Grunsven, R. H. A., Donners, M., Gienapp, P., Huigens, M. E., Slaterus, R., Berendse, F., Visser, M. E., & Veenendaal, E. (2015). Experimental illumination of natural habitat—an

- experimental set-up to assess the direct and indirect ecological consequences of artificial light of different spectral composition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370(1667), 20140129. <https://doi.org/doi:10.1098/rstb.2014.0129>
- Tamir, R., Lerner, A., Haspel, C., Dubinsky, Z., & Iluz, D. (2017). The spectral and spatial distribution of light pollution in the waters of the northern Gulf of Aqaba (Eilat). *Scientific Reports*, 7(1), 42329. <https://doi.org/10.1038/srep42329>
- Thayer, G. H. (1918). *Concealing-coloration in the animal kingdom: an exposition of the laws of disguise through color and pattern*. Macmillan Company.
- Tidau, S., Smyth, T., McKee, D., Wiedenmann, J., D'Angelo, C., Wilcockson, D., Ellison, A., Grimmer, A. J., Jenkins, S. R., & Widdicombe, S. (2021). Marine artificial light at night: An empirical and technical guide. *Methods in Ecology and Evolution*, 12(9), 1588-1601.
- Tidau, S., Whittle, J., Jenkins, S. R., & Davies, T. W. (2022). Artificial light at night reverses monthly foraging pattern under simulated moonlight. *Biology Letters*, 18(7). <https://doi.org/10.1098/rsbl.2022.0110>
- 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(4), 781-789.
- Wilbur, A. K., & Steneck, R. S. (1999). Polychromatic Patterns of *Littorina obtusata* on *Ascophyllum nodosum*: Are Snails Hiding in Intertidal Sea Weed? *Northeastern Naturalist*, 6(3), 189-198. <https://doi.org/10.2307/3858593>
- Williams, G. A. (1992). The effect of predation on the life histories of *Littorina obtusata* and *Littorina mariae*. *Journal of the Marine Biological Association of the United Kingdom*, 72(2), 403-416.
- Zissis, G., & Bertoldi, P. (2014). 2014 Update on the Status of LED market. In: Publications Office of the European Union.

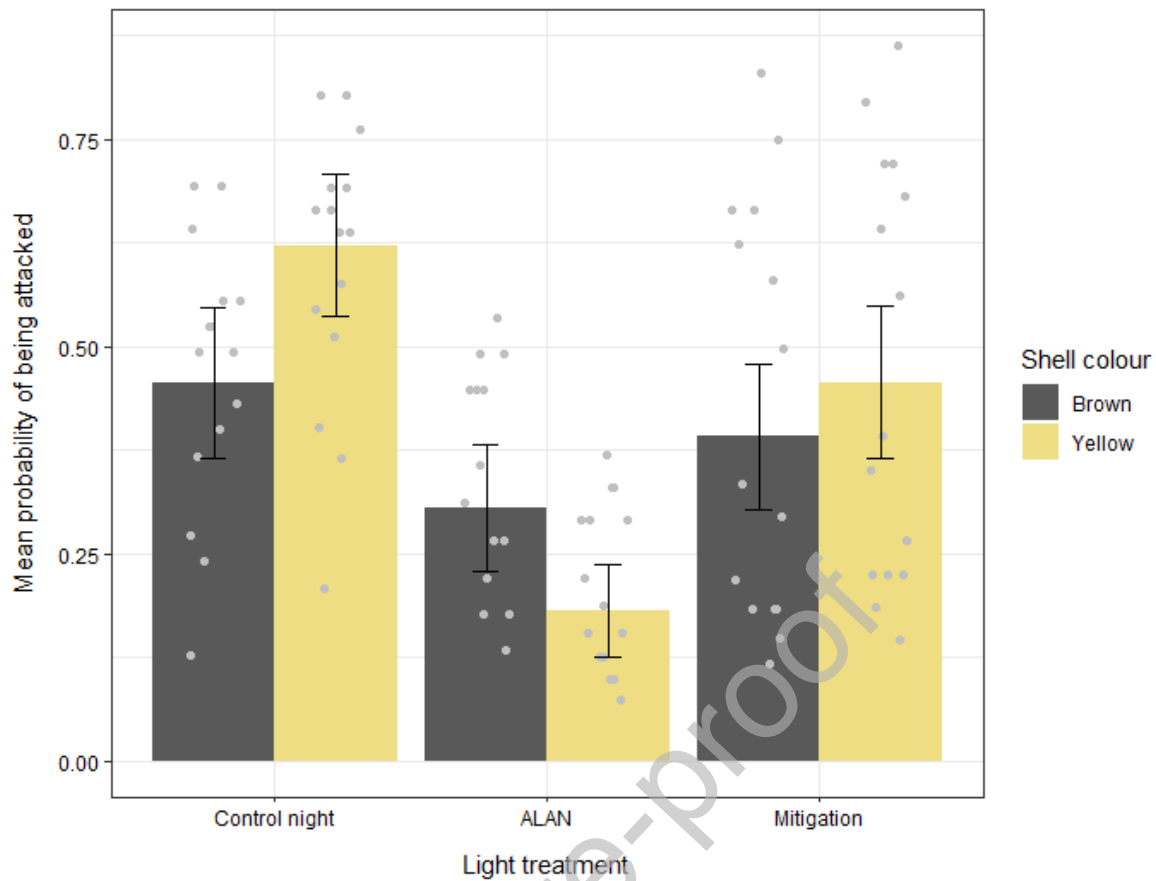


Fig. 1. The impact of three light treatments on the probabilities of two contrasting colour morphs of *Littorina obtusata* being attacked by *Carcinus maenas*. Plot is derived from estimated marginal means based on fitted binomial generalised linear mixed-effects models. Bars represent model means; error bars represent standard errors. Grey dots represent raw predicted probabilities.

Table 1. Impact of light treatment and shell colour on attack probability in *Littorina obtusata*.

Significant main effects and interactions are in italics.

Main effects and interactions	χ^2	d.f.	<i>p</i>
<i>Treatment</i>	6.971	2	0.031
Colour	0.4004	1	0.527
<i>Treatment*Colour</i>	12.785	2	0.002

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Table 2. Results of post-hoc pairwise comparisons of attack probability between *Littorina obtusata* shell colours (brown vs. yellow) by light treatment. Significant differences are in italics.

Treatment	Estimate	SE	d.f.	z ratio	p
<i>ALAN</i>	<i>0.689</i>	<i>0.281</i>	<i>Inf.</i>	<i>2.454</i>	<i>0.035</i>
<i>Control night</i>	<i>-0.676</i>	<i>0.270</i>	<i>Inf.</i>	<i>-2.501</i>	<i>0.035</i>
Mitigation	-0.268	0.278	Inf.	-0.967	0.417

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Table 3. Results of post-hoc pairwise comparisons of overall attack probability of *Littorina obtusata* by light treatment. Significant differences are in italics.

Treatment comparison	Estimate	SE	d.f.	z ratio	<i>p</i>
<i>ALAN – Control night</i>	<i>-1.297</i>	<i>0.476</i>	<i>Inf.</i>	<i>-2.724</i>	<i>0.019</i>
ALAN – Mitigation	-0.834	0.477	Inf.	-1.749	0.121
Control night – Mitigation	0.462	0.475	Inf.	0.973	0.331

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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