2022-07-27

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http://hdl.handle.net/10026.1/19408

Artificial light at night reverses monthly foraging pattern under simulated moonlight

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12   Abstract

13   Mounting evidence shows that artificial light at night (ALAN) alters biological processes across levels

14   of organisation, from cells to communities. Yet, the combined impacts of ALAN and natural sources

15   of night-time illumination remain little explored. This is in part due the lack of accurate simulations

16   of the complex changes moonlight intensity, timing, and spectra throughout a single night and lunar

17   cycles in laboratory experiments. We custom-built a novel system to simulate natural patterns of

18   moonlight to test how different ALAN intensities affect predator-prey relationship over the full lunar

19   cycle. Exposure to high intensity ALAN (10 and 50lx) reversed the natural lunar guided foraging

20   pattern by the gastropod mesopredator *Nucella lapillus* on its prey *Semibalanus balanoides*.

21   Foraging decreased during brighter moonlight in naturally lit conditions. When exposed to high

22   intensity ALAN, foraging increased with brighter moonlight. Low intensity ALAN (0.1 and 0.5lx) had

23   no impact on foraging. Our results show that ALAN alters the foraging pattern guided by changes in

24   moonlight brightness. ALAN impacts on ecosystems can depend on lunar light cycles. Accurate

25   simulations of night-time light cycle will warrant more realistic insights into ALAN impacts and also

26   facilitate advances in fundamental night-time ecology and chronobiology.

Introduction

Ecological light pollution is now an established field of global change research [1]. Satellite night-time imagery illustrates unequivocally the vast global extent of artificial light at night (ALAN). At least 80% of the world's population is exposed to ALAN [2] and its influence is expanding both in area (2.2% per year) and intensity (1.8% per year) [3]. Mounting evidence shows that ALAN alters biological processes across levels of organisation, from cells to communities, and across a range of biomes, taxa and spatial scales [4, 5]. Accurate prediction and mitigation of ALAN impacts demand a deeper understanding of how they are modified by other factors that shape the natural night-time light environment and biological adaptations to them.

The moon is the single most important source of environmental night-time illumination. It drives large-scale ecosystem processes and a diverse array of physiological and behavioural rhythms [6], the most widely known being lunar entrained global synchronised mass spawning in corals [7]. Lunar driven phenological life-history events such as reproduction and migration are found across the animal kingdom in marine [8-11], terrestrial [12, 13] and freshwater [14, 15] habitats across the globe. Lunar rhythms influence organisms' growth [16] and activity patterns [12]. Moonlight intensity affects communication [13], orientation [17] and risk-reward trade-offs [18, 19]. Recent research suggests that ALAN interferes with lunar guided migration [20], orientation [21], sleep time [22] and reproduction [23] at intensities similar to natural moonlight.

Current evidence of ALAN disrupted lunar biology is often limited to characterising only the moon phases, which do not reflect the lunar cues organisms are likely to detect in the wild. Moon phases describe the lunar cycle as the portion of illuminated lunar disc as observed from Earth and suggest a sinusoidal pattern in lunar intensity when, in reality, the pattern of changes in lunar brightness throughout a cycle follows extreme peaks and troughs as the moon transits the sky [Fig 1; 24]. Lunar intensity varies throughout the night, with day, month, year and enneadecaeteris (the ~19 year metonic cycle) for any location and time, owing to variations in lunar phase angle, altitude and atmospheric scattering (Fig 1A & B) [25, 26].

We built a novel system that allows us to quantify the ecological impacts of ALAN over a full lunar cycle simulating the timing and intensity of moonlight as experienced in nature. Rather than simulating sinusoidal changes in lunar phases, our system simulates natural night-time conditions for a specified location and date (Fig 1B & C). We exposed the gastropod mesopredator *Nucella lapillus* to a range of seven ALAN intensities, from low levels within the range of natural lunar light intensities (0.1 and 0.5lx), up to levels (10 and 50lx) similar to those experienced by organisms close to ports, harbours and street lights [27]. We measured the foraging probability of *Nucella* on its

60   prey, the barnacle *Semibalanus balanoides*, over an entire lunar cycle. We asked a) whether ALAN

61   impacts vary over the lunar cycle; b) whether ALAN impacts are expressed during the night or

62   daytime; and c) whether ALAN impacts change over the duration of the experiment (due to

63   acclimation).

64

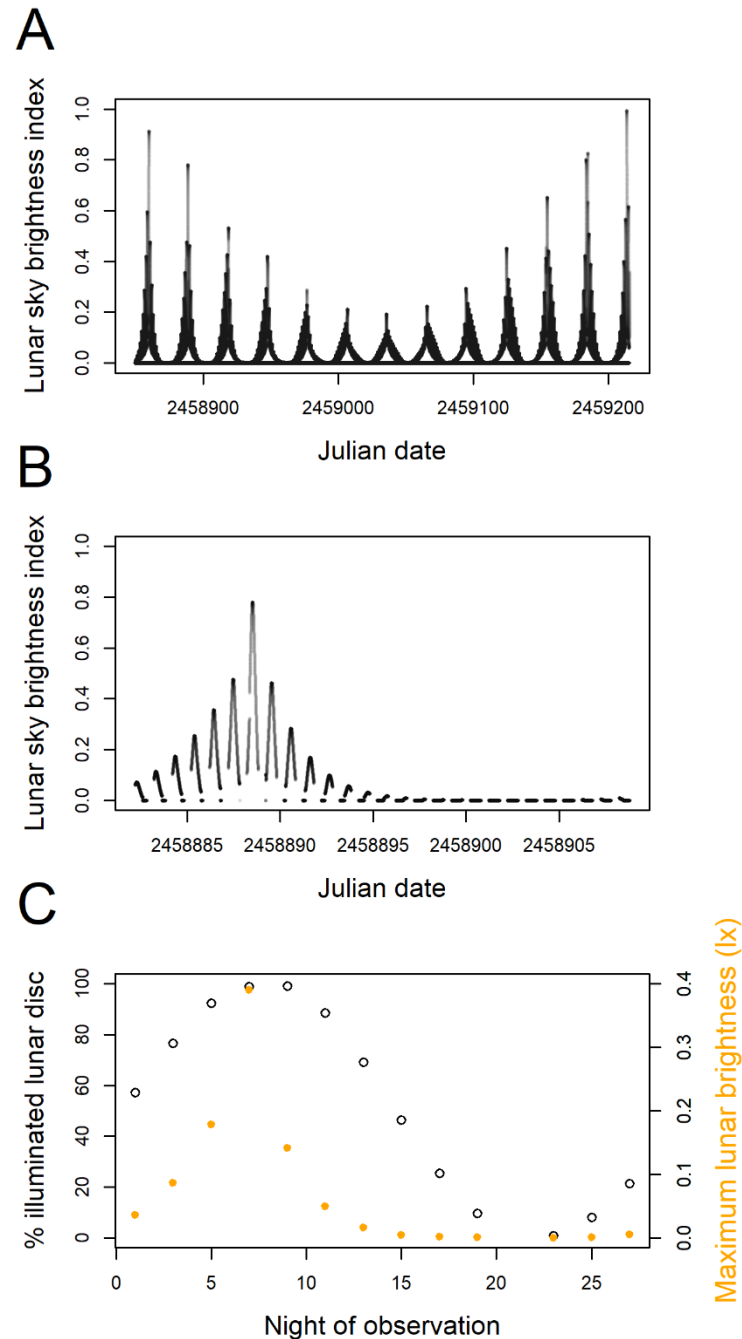**Figure 1 Lunar cycle in nature and in the laboratory for Menai Bridge, UK. A) Lunar cycle in nature**
over 12 month in 2020 (astronomical unit Julian date, days elapsed since January 1st 4713 BC) as
lunar sky brightness index (normalised to 1 = 0.5lx); B) Lunar cycle in nature over the course of the
experiment (February 2nd – March 2nd) as lunar sky brightness index (normalised to 1 = 0.5lx); C)

69 **Lunar cycle in the laboratory as percentage illuminated disc following a sinosodial pattern (circles,**
70 **left y-axis) and as maximum lunar brightness (in lx) (closed points, right y-axis).**

71

72 Methods

73 *Nucella* were collected from an artificial light naive shore on the island of Anglesey, UK (53°11'6"N,

74 4°29'35"W) on 31st of January 2020, and transported to the School of Ocean Sciences, Menai Bridge,

75 UK (53°13'57"N, 4°10'22"W). Individuals were sexed, and male *Nucella* marked for individual

76 identification and assigned to one of seven light treatment chambers (no ALAN, 0.1lx, 0.5lx, 1lx, 10lx,

77 10lx mitigation and 50lx). Each 0.16m^3 light treatment chamber contained three 2l clear Perspex

78 tanks (*n* = 21; 20L x 12W x 13H cm), each of which housed 4 individuals (*n* = 84) in 0.5μm filtered UV

79 irradiated seawater changed every second day. *Nucella* had ad libitum access to rocks (ca. 50 cm^2

80 surface area, < 5% of the total 1,072cm^2 available tank surface area) covered with their prey, the

81 barnacle *Semibalanus balanoides*, replaced every four days.

82 The natural daylight and moonlight regimes experienced by *Nucella* on their native shore were

83 simulated in each chamber. Daylight was simulated using an Aquaray Natural Daylight Tile set at

84 5000lx (mean 4781lx +/- 5%) and the BioLumen Control Unit (Tropical Marine Centre, UK)

85 programmed in real time to the sunrise and sunset times of Menai Bridge, UK (53°13'57"N,

86 4°10'22"W). To evenly diffuse the light and minimise bright spots [4], the daylight tile was covered

87 by 3mm frosted Perspex. Moonlight regimes were simulated using a bank of 2700-3500K 1.2 cd LEDs

88 housed within diffusing spheres to minimise light spots. Natural moonlight regimes were simulated

89 using a Pulse Width Modulated signal (scale 0-100%) applied to the 5V output of Raspberry Pi 3

90 model B+, with maximum lunar brightness set to 0.5lx (observable within 2020, Fig 1A). Lunar

91 brightness was adjusted from a look up table (1 minute resolution) of Zenith Sky Brightness

92 modelled for Menai Bridge. Modelling followed [27] whereby the moon's sky position and phase

93 angle are calculated from the time, date and geocentric coordinates of location (CRAN: astrolib). The

94 Zenith Sky Brightness is then modelled accounting for lunar phase, altitude, opposition, parallax and

95 atmospheric scattering according to [28]. Uniquely, in comparison to previous lunar simulations

96 under experimental laboratory settings, our system captures variability in night-time lighting as the

97 moon transits the sky [25, 26]. The spectrum of moonlight changes throughout the night with lunar

98 phase and elevation [29, 30]. As with twilight, this persists to be technically challenging [4] and

99 hence was not manipulated. ALAN was simulated between dawn and dusk (triggered using a

100 CellOptick 12V photocell) using Aquaray cool white FlexiLED strips (Tropical Marine Centre, UK), with

101 brightness controlled using voltage dimming. As the lens eyes [31] of aquatic gastropods typically

102   show peak spectral sensitivity from 470 to 505nm [32, 33], we evaluated a potential mitigation

103   solution using a long band pass (510nm–2200nm) yellow acrylic filter (www.knightoptical.com),

104   which minimises blue wavelengths prominent in LEDs. This was implemented in one of two 10lx

105   treatment chambers.

106   Behaviour was observed over one lunar cycle between February 2nd and March 2nd 2020 using

107   infrared time-lapse photography. GoPro Hero 4 cameras fitted with infrared pass lenses were

108   programmed with Blink Time Lapse Controllers for GoPros (CamDo, USA) to take one photo every

109   five minutes for 24 hours every second night over the 28 day period (= 289 photos per 24 hours, for

110   each of the 7 treatments, each of the 12 individually marked animals per treatment, for 13 nights of

111   observation = up to 315,588 photos. Due to a charging error, there are no observations for day 21,

112   see Fig 1C). This sampling frequency allowed the recording system to last for 24 hours (from 15:00

113   day 1 to 15:00 day 2) and to capture 13 nights without interruption over one lunar cycle. Images

114   were down-sampled from colour to 8-bit grayscale with ImageJ. Brightness and contrast were

115   adjusted to maximise visibility. Images were converted into a single time-lapse video for each 24

116   hour. Due to naturally high levels of inactivity in *Nucella*, we classed their behaviour as either

117   foraging (when sitting on the rock with barnacles) or not foraging (when not sitting on a rock). This is

118   a common metric for gastropod foraging and avoids disturbing animals [34-37]. We also recorded

119   whether the behaviour occurred day and/ or night-time leading to two data points per individual per

120   video. Due to the persistent technical challenges in simulating twilight timing, spectra and intensity

121   [4], we excluded footage taken over dusk and dawn.

122   We quantified whether *Nucella*'s foraging activity (binary: Foraging/Not Foraging) was affected by

123   ALAN (categorical: 0, 0.1, 0.5, 1, 10, 10 mitigation, 50lx) in interaction with either a) moonlight

124   intensity (continuous: maximum lunar brightness per night; Fig 1C), b) time of day (categorical: night

125   or day), and c) experimental day i.e. night of observation (continuous: night 1-27) using R (version

126   4.1.2). The latter explored potential collinear effects that may arise due to *Nucella* acclimatising. To

127   find the most parsimonious model, we first fitted a global binomial generalised linear model (GLM)

128   with the following interactions: ALAN*Moonlight + ALAN*NightofObservation + ALAN*TimeofDay.

129   Next, we used the dredge function (CRAN: MuMIn) which automates model selection through

130   subsetting the maximum model based on model weights derived from Akaike's Information Criterion

131   (AICs). The model explaining < 99% of the response based on weight and the lowest AICs included

132   ALAN*Moonlight + ALAN*NightofObservation + TimeofDay (see Table S1 for all models). This most

133   parsimonious GLM was compared to a intercept only model for validation using a likelihood ratio

134   test [38]. Since the GLM explained significantly more variance in the response than the intercept

135   only model (χ^2 = -80.58, df = 21, p < 0.001), the GLM was refitted as generalised linear mixed effects

136   (GLMM) model (CRAN: lme4). Snail ID was nested in tank as a random factor to account for the

137   experimental design. The significance of the GLMM parameters was quantified using the Type III

138   ANOVA approach of stepwise model selection [39]. Again, models were compared using likelihood

139   ratio tests. Significant difference between treatment levels were quantified by pairwise comparisons

140   using the emtrends function (CRAN: emmeans) which allows to include a numerical predictor (here

141   Moonlight) interacting with a factorial predictor (here ALAN). We did not adjust p-value to avoid

142   inflating the Type I error. The predicted relationships and their 95% intervals were modelled for

143   visual presentation using the predictInterval function (CRAN: merTools).

Results

145   Foraging activity was influenced by the nightly maximum lunar brightness, however, the direction of

146   this relationship was significantly affected by exposure to different ALAN treatment levels

147   (ALAN*Moonlight: χ^2 = 33.67, df = 6, p < 0.001; Fig 2; Table 1, Table S2). Under natural night-time

148   light simulations (no ALAN), *Nucella* were less likely to forage on brightly moonlit nights, while under

149   high intensity ALAN (10 and 50lx), *Nucella* were more likely to forage on brightly moonlit nights (Fig

150   2). Foraging activity in *Nucella* exposed to the mitigation treatment (filtered out light under 510nm)

151   differed from both the 10lx treatment and control conditions (Fig 2; Table S2). (Fig 2; Table S2). The

152   impact of ALAN on foraging was affected by night of observation (χ^2 = 17.29, df = 6, p = 0.008; Table

153   1, S3). Time of day had no effect on foraging (χ^2 = 0.18, df = 1 , p = 0.670).

154   **Table 1 The impact of artificial light at night, lunar brightness, night of observation and time of day**
155   **on foraging in *Nucella lapillus*. Significant main effects and interactions are in bold.**

Factor	χ^2	df	p
ALAN*Moonlight	**33.67**	**6**	**< 0.001**
ALAN*Night of Observation	**17.29**	**6**	**0.008**
ALAN	4.89	6	0.558
Moonlight	1.74	1	0187
Night of Observation	**10.41**	**1**	**0.001**
Time of Day	0.18	1	0.670
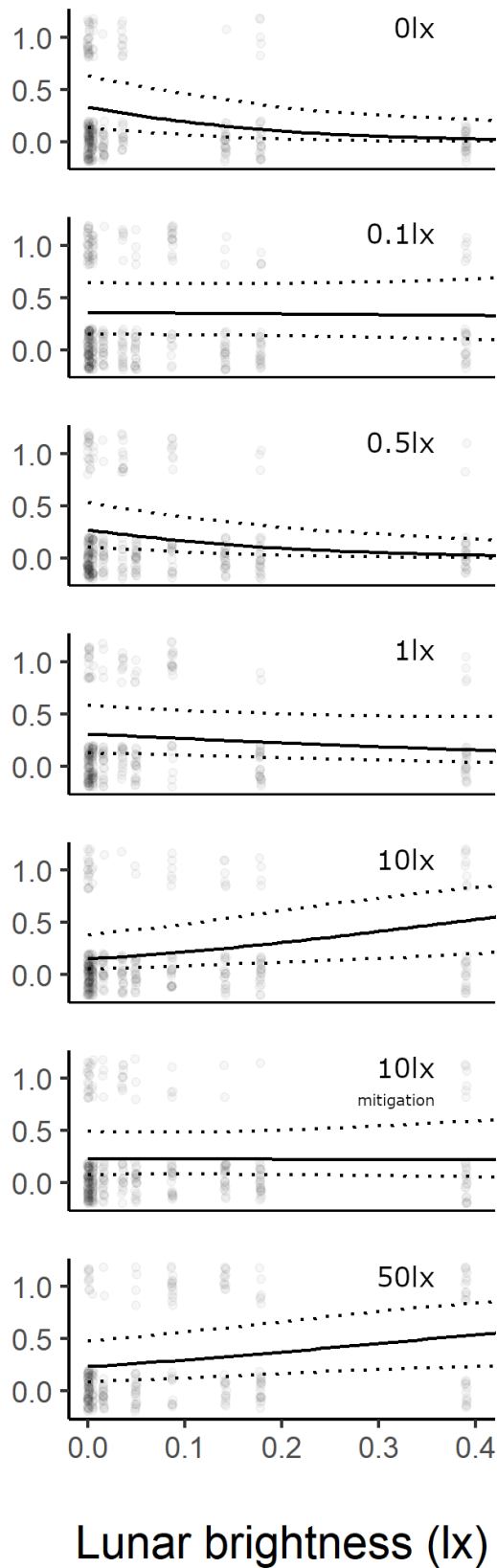
Figure 2 The interactive impact of different ALAN intensities and maximum lunar brightness on foraging occurrence in *Nucella lapillus*. The figure shows the raw data (jittered dots), predicted relationships (solid line) and 95% prediction intervals (dotted lines).

Discussion

160

161   Artificial light at night (ALAN) is known to affect lunar guided reproductive phenology [23],

162   orientation [20, 21] and community structure [19]. Our results demonstrate that ALAN can also alter

163   temporal patterns in foraging tuned to the naturally changing nightly lunar brightness throughout

164   the lunar cycle.

165   Under the simulation of natural moonlight, *Nucella* foraged less with increasing moonlight intensity.

166   Suppressed activity on brighter moonlit nights is a common pattern driven by risk-reward trade-offs

167   [12, 18, 19]. High intensity ALAN levels, however, reversed this pattern. *Nucella* was more likely to

168   forage during brighter moonlit nights under ALAN intensities of 10 and 50lx. The gastropod sensory

169   system allows *Nucella* to use chemical and visual channels to detect prey (mussels and barnacles)

170   and predators (crabs and birds) [33, 40]. The high intensity ALAN treatments masked the maximum

171   lunar brightness attained on any night during the experiment (0.39lx) and could have been bright

172   enough for *Nucella* to visually exclude predation risk. This interpretation aligns with previous

173   observations of *Nucella* foraging in the presence of predator olfactory cues when exposed to ALAN

174   but not in dark control treatments [41]. ALAN intensities of 0.5 and 1lx, which are similar to artificial

175   skyglow [20], could be too dark to allow accurate visual assessment of the environment and risk

176   perception.

177   A growing body of evidence indicates that ALAN has notable impacts on lunar guided biological

178   process [18-21, 23]. Here we show that ALAN impacts also depend on natural regimes of lunar

179   brightness. The brightness of naturally lit nights is a function of lunar phase, altitude and scattering,

180   yet studies investigating both ALAN impacts and chronobiological responses to moonlight simulate

181   the sinusoidal pattern of lunar phase at best [26, 42, 43]. Moonlight intensity does not change in a

182   sinusoidal pattern, as suggested by lunar phases, which give the portion of illuminated lunar disc as

183   observed from Earth. The full moon is 1.3 times brighter than can be accounted for solely by the

184   increase in percentage of illuminated lunar disc due to the so-called lunar opposition effect. This

185   phenomenon describes the non-linear intensity increase with decreasing phase angle [25, 27, 28]. In

186   nature, animals hardly experience maximum lunar brightness between 0.2 and 0.4lx. To quantify

187   biologically relevant ALAN impacts on organisms over a lunar cycle requires simulating the lunar

188   intensity accurately. Resolving technical challenges in mimicking the spectral composition of

189   moonlight [28, 30] will facilitate further mechanistic insight also into crepuscular processes [6, 7] and

190   ALAN disruptions to them. ALAN research is increasingly embedded into a multisensory pollution

191   approach [19, 44] to assess its interactions with other anthropogenic stressors like noise [45, 46] and

192   warming [47]. Future research that aims to facilitate a better understanding of anthropogenic

193 impacts on wildlife should also consider how these interact with natural factors. For ALAN research,

194 this means first and foremost lunar cycles described by temporal variability in moonlight intensity

195 through the night, month, year and enneadecaeteris. Our results highlight the importance of

196 accounting for moonlight when investigating ALAN impacts. In the laboratory setting, this means

197 accurately simulating moonlight. Doing so will provide novel mechanistic insights in the fields of

198 ecological light pollution, visual ecology, night-time ecology, and chronobiology; and improve the

199 application of experimental results to the real world.

Author contributions

207 ST, JW, SJ and TD designed the study. JW and ST conducted the fieldwork and data collection. ST and

208 TW analysed the data. ST wrote the first draft with all authors contributing to writing and approval

209 of the final version.

210 The data are provided in the electronic supplementary material [48].

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349

Tidau et al. 2022 Artificial light at night reverses monthly foraging pattern under simulated moonlight

Supplementary material 1 - Model Outputs

Table S1 Selection of the most parsimonious models describing foraging occurrence in Nucella lapillus. Top 4 models (in bold) account for > 99% weight.

Intercept only	ALAN	Moonlight	Night of Observations	Time of Day	ALAN * Moonlight	ALAN * Night of Observation	ALAN * Time of Day	df	AICc	weight
-0.85827	**+**	**-6.76216**	**-0.01941**	**NA**	**+**	**+**	**NA**	**21**	**1920.176**	**0.553489**
-0.83496	**+**	**-6.76257**	**-0.01941**	**+**	**+**	**+**	**NA**	**22**	**1922.058**	**0.216096**
-0.74902	**+**	**-7.14412**	**-0.02564**	**NA**	**+**	**NA**	**NA**	**15**	**1922.662**	**0.159699**
-0.72587	**+**	**-7.14456**	**-0.02564**	**+**	**+**	**NA**	**NA**	**16**	**1924.532**	**0.062702**
-1.20403	+	-5.60636	NA	NA	+	NA	NA	14	1929.662	0.004824
-1.181	+	-5.6067	NA	+	+	NA	NA	15	1931.53	0.001895
-0.75522	+	-6.77049	-0.01944	+	+	+	+	28	1933.322	0.000774
-0.64602	+	-7.15162	-0.02566	+	+	NA	+	22	1935.73	0.000232
-1.81519	+	NA	0.022114	NA	NA	+	NA	14	1936.763	0.000139
-1.74053	+	-0.39783	0.018876	NA	NA	+	NA	15	1938.35	6.26E-05
-1.79231	+	NA	0.022116	+	NA	+	NA	15	1938.632	5.44E-05
-1.71763	+	-0.39787	0.018878	+	NA	+	NA	16	1940.221	2.46E-05
-1.10162	+	-5.61325	NA	+	+	NA	+	21	1942.719	7.05E-06
-1.19171	+	NA	-0.02093	NA	NA	NA	NA	8	1947.315	7.08E-07
-1.16907	+	NA	-0.02093	+	NA	NA	NA	9	1949.174	2.80E-07
-1.15217	+	-0.22053	-0.02258	NA	NA	NA	NA	9	1949.192	2.77E-07
-1.71615	+	NA	0.022149	+	NA	+	+	21	1949.827	2.02E-07
-1.12952	+	-0.22055	-0.02258	+	NA	NA	NA	10	1951.052	1.09E-07
-1.64142	+	-0.39811	0.018909	+	NA	+	+	22	1951.429	9.05E-08
-1.14733	NA	NA	-0.02079	NA	NA	NA	NA	2	1953.621	3.02E-08
-1.48539	+	NA	NA	NA	NA	NA	NA	7	1953.767	2.81E-08

Intercept only	ALAN	Moonlight	Night of Observations	Time of Day	ALAN * Moonlight	ALAN * Night of Observation	ALAN * Time of Day	df	AICc	weight
-1.52999	+	0.603712	NA	NA	NA	NA	NA	8	1954.301	2.15E-08
-1.12489	NA	NA	-0.02079	+	NA	NA	NA	3	1955.47	1.20E-08
-1.11918	NA	-0.16382	-0.022	NA	NA	NA	NA	3	1955.548	1.15E-08
-1.46286	+	NA	NA	+	NA	NA	NA	8	1955.625	1.11E-08
-1.50745	+	0.603763	NA	+	NA	NA	NA	9	1956.16	8.50E-09
-1.09674	NA	-0.16383	-0.022	+	NA	NA	NA	4	1957.398	4.58E-09
-1.41746	NA	NA	NA	NA	NA	NA	NA	1	1960.123	1.17E-09
-1.09201	+	NA	-0.02094	+	NA	NA	+	15	1960.314	1.07E-09
-1.46544	NA	0.636885	NA	NA	NA	NA	NA	2	1960.457	9.91E-10
-1.39514	NA	NA	NA	+	NA	NA	NA	2	1961.97	4.65E-10
-1.05245	+	-0.22065	-0.02259	+	NA	NA	+	16	1962.205	4.14E-10
-1.4431	NA	0.636938	NA	+	NA	NA	NA	3	1962.306	3.93E-10
-1.38629	+	NA	NA	+	NA	NA	+	14	1966.757	4.25E-11
-1.43085	+	0.604113	NA	+	NA	NA	+	15	1967.304	3.23E-11

Table S2 Posthoc contrasts of the impact of ALAN * Moonlight (expressed as maximum lunar brightness) on foraging occurrence in *Nucella lapillus*. Significant results are in bold (using pairwise comparisons).

Contrasts	Estimate	SE	z	p
0 – 0.1	**-6.99**	**3.21**	**-2.18**	**0.029**
0 – 0.5	-0.55	3.83	-0.14	0.887
0 – 1	-4.90	3.31	-1.49	0.136
0 – 10	**-11.96**	**3.24**	**-3.69**	**<0.001**
0 – 10M	**-7.20**	**3.31**	**-2.18**	**0.030**
0 – 50	**-10.88**	**3.29**	**-3.31**	**<0.001**
0.1 – 0.5	**6.45**	**2.98**	**2.17**	**0.030**
0.1 – 1	2.06	2.26	0.91	0.363
0.1 – 10	**-4.97**	**2.16**	**-2.30**	**0.021**
0.1 – 10M	-0.20	2.25	-0.09	0.928
0.1 – 50	-3.89	2.22	-1.75	0.080
0.5 – 1	-4.39	3.08	-1.42	0.155
0.5 – 10	**-11.41**	**3.01**	**-3.79**	**<0.001**
0.5 – 10M	**-6.65**	**3.08**	**-2.16**	**0.031**
0.5 – 50	**-10.34**	**3.06**	**-3.38**	**<0.001**
1 – 10	**-7.02**	**2.31**	**-3.047**	**0.002**
1 – 10M	-2.26	2.40	-0.94	0.346
1 – 50	**-5.95**	**2.37**	**-2.51**	**0.012**
10 – 10M	**4.76**	**2.30**	**2.07**	**0.038**
10 – 50	1.08	2.27	0.48	0.635
10M – 50	-3.69	2.36	-1.56	0.119

Table S3 Table S3 Posthoc contrasts of the impact of ALAN * Day of observation on foraging occurrence in Nucella lapillus. Significant results are in bold (using pairwise comparisons).

| Contrasts	Estimate	SE	z	p
0 – 0.1	-0.03	0.03	-0.82	0.411
0 – 0.5	0.06	0.03	1.75	0.081
0 – 1	0.39	0.03	1.16	0.246
0 – 10	-0.04	0.04	-1.29	0.199
0 – 10M	-0.02	0.03	-0.46	0.644
0 – 50	0.06	0.03	1.42	0.155
0.1 – 0.5	**0.09**	**0.03**	**2.74**	**0.006**
0.1 – 1	**0.06**	**0.03**	**2.15**	**0.031**
0.1 – 10	-0.02	0.03	-0.61	0.545
0.1 – 10M	0.01	0.03	0.35	0.728
0.1 – 50	**0.08**	**0.04**	**2.20**	**0.028**
0.5 – 1	-0.02	0.03	-0.66	0.512
0.5 – 10	**-0.11**	**0.04**	**-3.00**	**0.003**
0.5 – 10M	**-0.08**	**0.03**	**-2.27**	**0.023**
0.5 – 50	<0.00	0.04	-0.07	0.945
1 – 10	**-0.08**	**0.03**	**-2.48**	**0.013**
1 – 10M	-0.05	0.03	-1.69	0.091
1 – 50	0.02	0.04	0.49	0.629
10 – 10M	0.03	0.03	0.88	0.380
10 – 50	**0.10**	**0.04**	**2.51**	**0.012**
10M – 50	0.07	0.04	1.85	0.064

Supplementary file S2 Spectral Measurements
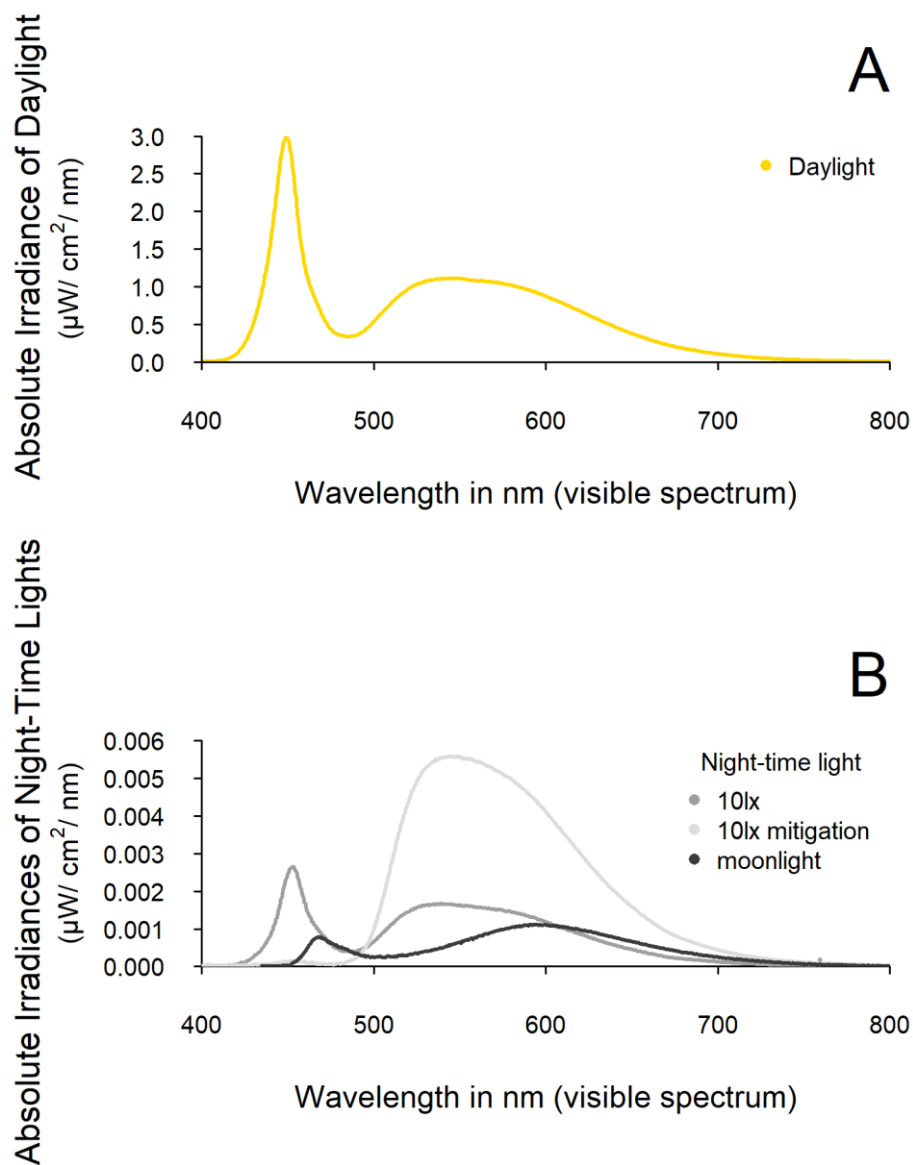
Figure S2 Spectral outputs day and night-time light sources as absolute irradiance (µW/ cm2/ nm) within the visible range of 400-800 µm

Table S2 Energy content of the spectral outputs of day and night-time light sources as absolute irradiance (µW/ cm^2/ nm) within the visible range of 400-800 µm.

	Daylight	Moonlight	10lx ALAN	10lx ALAN mitigation
Total absolute irradiance	481.1601	0.3615943	0.5868144	1.471918
Peak absolute irradiance	2.992874 at 449.3 nm	0.001123044 at 590.62	0.002654932 at 452.70	0.005589028 at 547.80 nm