

2022-11-09

Under the influence of light: How light pollution disrupts personality and metabolism in hermit crabs

Velasque, M

<http://hdl.handle.net/10026.1/19965>

10.1016/j.envpol.2022.120594

Environmental Pollution

Elsevier BV

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

Under the influence of light: how light pollution disrupts personality and metabolism in hermit crabs

Velasque, M.^{1,2,3*} Denton, J.A.⁴, & Briffa, M.¹

1. School of Biological and Marine Sciences, University of Plymouth, Plymouth, Devon, United Kingdom

2. Genomics & Regulatory Systems Unit, Okinawa Institute of Science & Technology, Okinawa, Japan

3. The Experimental Evolutionary Biology Lab, School of Biological Sciences, Monash University, Clayton, Victoria, Australia

4. The World Mosquito Program, Institute of Vector-borne Disease, Monash University, Clayton, Victoria, Australia

* mari.velasque@monash.edu

PRE-PRINT

Version of record: <https://doi.org/10.1016/j.envpol.2022.120594>

Published in *Environmental Pollution*.

Highlights

- Coastal zones are highly affected by light pollution
- Constant light reduced boldness and increased metabolism in hermit crabs
- Behavioural and metabolic changes can affect population stability
- Light pollution might disrupt hermit crab populations changing intertidal diversity

Abstract

Anthropogenic disturbances are known to cause significant physiological and behavioural changes in animals and, thus, are the critical focus of numerous studies. Light pollution is an increasingly recognised source of disturbance that has the potential to impact animal physiology and behaviour. Here, we investigate the effect of constant light on a personality trait and metabolic rate in the European hermit crab *Pagurus bernhardus*. We used Bayesian mixed models to estimate average behavioural change (i.e. sample mean level behavioural plasticity) and between- and within-individual variation in boldness in response to laboratory light. Hermit crabs experiencing constant light were consistently less bold and had a higher metabolic rate than those kept under a standard laboratory light regime (12:12h light/dark). However, there was no effect of light on individual consistency in behaviour. As boldness is associated with coping with risk, hermit crabs exposed to light pollution at night may experience increased perceived predation risk, adjusting their behaviour to compensate for the increased conspicuousness. However, reduced boldness could lead to lower rates of foraging and this, in combination with elevated metabolic rate, has the potential for a reduction in energy balance.

Keywords

Light pollution, artificial light at night, animal personality, environmental change

Introduction

In natural environments, light regimes follow predictable and cyclic patterns of change. This predictability favoured the evolution of mechanisms that allow animals to anticipate and react to changes in light conditions (Burgess and Marshall, 2014; Lines et al., 2012; Tuomainen and Candolin, 2011), such as adapting their behaviour and physiology according to the duration of the day (Gaston et al., 2013; Hut and Beersma, 2011). For intertidal animals, light availability and brightness carry additional information: changes in lunar brightness caused by the moon cycle help animals to anticipate changes in current velocity and tidal height (Davies et al., 2014; Naylor, 2010; Truscott et al., 2017). However, artificial light at night (ALAN) can mask seasonal and monthly fluctuations in sky brightness regimes and thus interfere with these cues.

There is increasing evidence that ALAN can alter physiology (Forsburg et al., 2021; Luarte et al., 2016; Raap et al., 2016a; Zubidat et al., 2018), metabolism (Finch et al., 2020; Nelson, 2019; Raap et al., 2018a; Welbers et al., 2017), foraging (Davies et al., 2013; Farnworth et al., 2018) reproduction and mating behaviour (Ayalon et al., 2021; Botha et al., 2017; Degen, 2015; Touzot et al., 2019), often in a species specific manner (Amadi et al., 2021; Baskir et al., 2021; Brisbane and van den Burg, 2020; Polak et al., 2011), making understanding ALAN's impacts challenging. However, changes in physiology and behaviour could alter interspecific dynamics, having significant ecological consequences disrupting entire ecological communities (Bennie et al., 2018; Sanders et al., 2018, 2015). In addition, ALAN was also shown to disrupt metabolic rate, increasing organisms' energy requirement and food consumption, which can further alter the stability of the food web (Hillyer et al., 2021; Manríquez et al., 2019; Marangoni et al., 2022).

Consistent between-individual differences in behaviour, known as 'animal personality', are present in a wide variety of taxa (Bergmüller, 2010; Briffa and Weiss, 2010; Carter et al., 2013). Risk-taking behaviour, or 'boldness', is one of the most studied aspects of animal personality as it has direct fitness consequences (Bevan et al., 2018; Oosten et al., 2010; Westneat et al., 2013). For instance, consistent differences in boldness are linked with differences in survival (Bubac et al., 2018; White et al., 2013), reproductive success (Gasparini et al., 2019; Smith and Blumstein, 2008), predation pressure (Biro et al., 2006; Stamps, 2007), parental care (Reddon, 2012), foraging (Sneddon, 2003) and even to different life-history traits, such as growth (Finstad et al., 2007; Lantová et al., 2011). Thus, more active individuals also tend to be more aggressive, bolder and more explorative compared to less active individuals forming a pace-of-life syndrome (POLS; Careau et al., 2008; J. Galliard et al., 2013; Réale et al., 2010). Individuals with a faster POLS (i.e. higher activity, boldness and aggressiveness) also tend to have a higher energetic demand and consequently higher metabolic rates (Dammhahn et al., 2018; J.-F. L. Galliard et al., 2013).

Despite being one of the best-studied personality traits, little is known about how risk-taking behaviour (i.e. boldness) changes in response to environmental disturbances. This is particularly important as environmental changes, such as ALAN, can alter multiple aspects of

83 predator-prey dynamics. Their impact also varies with the intensity of environmental
84 disturbance, organism physiology and personality (i.e. pace of life; Belgrad et al., 2017; Pamela
85 Delarue et al., 2015). In addition to affecting an individual's mean boldness (and hence that of
86 the population; Kurvers et al., 2018; O'Connor et al., 2019), night-time light may also alter
87 behavioural plasticity itself (i.e. the extent to which individuals adjust their behaviour to match a
88 change in circumstance) and consistency, further increasing the variability across individuals in
89 how they respond to this stressor (Raap et al., 2018b, 2015).

90 In addition to boldness, light may also alter behavioural plasticity (i.e. mean level
91 adjustments to a change in circumstance) and consistency, increasing the variability with
92 individuals' respond to this stressor. For example, light can hamper the ability to assess risk,
93 which they might counter by behaving in more risk-averse ways, for example, by increasing
94 their behavioural variability (i.e. within or intra-individual variation and residual variance; see
95 Stamps et al., 2012; Westneat et al., 2015). Alternatively, it could alter how different individuals
96 within a population respond to risk, changing not only the population mean level response but
97 also the among-individual variation around such a mean (i.e. between individual variation or
98 behavioural reaction norms see Dingemanse et al., 2010). Alternatively, it could alter how
99 different individuals within a population respond to risk, changing a population level response
100 (i.e. between individual variation or behavioural reaction norms (Dingemanse et al., 2010)).
101 These effects would alter the repeatability of behaviour, the key marker for animal personalities.
102 However, the way in which ALAN alters individual and population-level behavioural expression
103 is not well known.

104 In arthropods, oxygen is transported by haemocyanin, analogous to haemoglobin in
105 vertebrates (Mangum 1985). Changes in the concentration of this protein are directly correlated
106 to an organism's changes in energetic demands and, thus, can provide a robust estimation of
107 long-term response to stressors (Spicer and Baden, 2000). For instance, an increase in
108 haemocyanin concentration could be associated with adaptations to an increased energetic
109 demand caused by an environmental stressor. Therefore, patterns of oxygen consumption can be
110 used as a proxy for energetic demand and activity to determine environmental factors that shape
111 metabolism (Hillyer et al., 2021; Manríquez et al., 2019; Marangoni et al., 2022; Spicer and
112 Baden, 2000)

113 Here, we investigated how light at night can disrupt animal personality and its variance
114 components (among and within individual variation in behaviour). As a model system, we used
115 *Pagurus bernhardus*. *P. bernhardus* is a diurnal species (Mitchell, 1973) and one of Europe's
116 most common intertidal decapods (Benedict, 1901; Lancaster, 1990). Although they can be
117 found in a wide range of environments and depths, younger individuals primarily inhabit the
118 intertidal, where they are extremely common in north-western Europe (Benedict, 1901; Elwood,
119 n.d.; Lancaster, 1990). Therefore, *P. bernhardus* is likely to be the species more frequently
120 affected by light pollution, especially in terms of its youngest and largest cohorts.

We were particularly interested in how both within-individual variances in boldness and population average boldness behaviour might be affected by exposure to consistent light at night. Personality traits are often correlated with energy consumption and metabolism (i.e. fast-slow life-history continuum; see Holtmann et al., 2017; Réale et al., 2010), a trait well known to be disrupted by ALAN (O'Connor et al., 2019; Pulgar et al., 2019) metabolic rate. We focused on two aspects of behavioural variation: between individuals (i.e. behavioural plasticity in response to a change in conditions) and within-individuals (i.e. behavioural consistency). We used haemocyanin concentration of hermit crabs and oxygen concentration as proxies for metabolism. As ALAN's effects on behaviour and physiology seem to be dependent on the organism's circadian rhythm (i.e. nocturnal vs diurnal; Dickerson et al., 2022; Le Tallec et al., 2013; Spoelstra et al., 2018), it is possible that any effects also influence day-time behaviour. Therefore, we investigated behavioural changes at two different time periods, day (i.e. during daylight hours) and night (i.e. during night-time hours). We predicted that hermit crabs would be aware of their conspicuousness (Briffa and Twyman, 2011) and adjust their behaviour, by decreasing boldness, in response to light at night. Furthermore, as *P. bernhardus* is a diurnal species (Mitchell, 1973), we expect a decrease in boldness during the night and an increase during the day when exposed to ALAN. In addition, we also expect that the increased perceived predation risk caused by ALAN would increase individual variation (i.e. decrease predictability) while decreasing overall variation within a population (i.e. among individual variation). We also predict that such a pattern would be conditioned to the time period, with day measurements being less variable than nights.

Methods

We collected hermit crabs from Hannaford Point, UK., an area with low light pollution levels and transported them to the lab. We removed crabs from their shells by cracking in a bench vice in the laboratory. This stage is necessary because hermit crabs' behaviour, including the startle response's duration, could be affected by the shell mass (Briffa and Bibost, 2009). All crabs thus received a new *Littorina littorea* shell with 100% of its preferred mass, calculated from a relationship between crab mass and preferred shell mass established during a previous shell-selection experiment (Briffa and Elwood, 2007). We only used adult male crabs (mean mass = 0.76 g \pm S.E. = 0.34 g) as females may change their shell preferences in unpredictable ways during the breeding season (Benedict, 1901; Lancaster, 1990). All hermit crabs were free from apparent parasites (such as Rhizocephalans) that generally attach to the abdomen or are present in the gill chambers, causing noticeable bulging of the carapace, appendage damage, or recent moult. Crabs were individually housed in white plastic dishes of 16 cm in diameter, filled to 4 cm depth with seawater, with continuous aeration, and fed daily ad libitum with cubes of white fish at the end of night-time measurements (i.e. there was always excess food available in the housing dishes, outside of the observation periods) and water was replaced daily.

Before all observations, all animals were housed in separate chambers with controlled light conditions to simulate either constant light or a 'standard light' regime. Standard light

treatment employed a 12:12h (7 am:7 pm) light: dark treatment, whereas constant light used the same intensity light for 24 hours. Those animals were left in either condition for a 10-day acclimation period, followed by ten days of observations (twice a day as described below). The startle response was measured on the 11th day following the acclimation, and on the 21st day, we reversed light conditions experienced by animals. Thus, all animals initially undergoing standard light treatment were transferred to constant light treatment and vice versa. We restarted observations after a 10-day acclimation period, followed by ten days of observations (Briffa and Bibost, 2009). We applied a crossover design (Briffa et al., 2013), as it is the standard approach in behavioural experiments involving repeated measures, where individuals are subject to more than one treatment.

Hermit crabs were kept under fluorescent lights (fluorescent tubes, white colour) with similar light conditions during the day (unpaired t-test $t_{24} = 0.11$, $p = 0.92$) and were on average 38.554 lux (range = 30.1- 44.6, $n_{\text{locations}} = 25$). In Hannaford Point, street lighting used high-pressure sodium lamps and varied across the shore, averaging 0.127 lux (range = 0 - 1.4, $n_{\text{locations}} = 25$). Although light conditions at the laboratory were higher and less variable when compared to Hannaford Point, the light intensity of 30-40 lux can also be considered conservative relative to developed coastal areas with high human influence (60-210 lux; Luarte et al., 2016; Pulgar et al., 2019).

Behavioural assays

We used a startle response as a proxy for boldness. We induced startle response (standard light, $N = 15$; constant light, $N = 15$, $N_{\text{total}} = 30$) using a handling protocol, where crabs were lifted out of their tank and replaced in an inverted position on the tank's base. This causes them to withdraw into their gastropod shell. We timed the recovery latency from the point at which the crab was replaced in the tank to when the walking legs were re-contacted with the tank's base (Briffa et al., 2008). Although many marine animals are assumed to be more active at night, *P. bernhardus* under standard light conditions (12:12h light: dark) is more active during the day than at night (peak of activity at 9:00 and lower activity at 22:30h (Mitchell, 1973). Therefore, we induced startle responses twice daily at 9:00 (day-time observations) and 21:00 (night-time observations) for 10 days in each experimental period. We made night-time observations under the 12:12h light: dark cycle with low levels of red light to avoid influencing crab behaviour (Hazlett, 1966; Sinn and Moltchanowskyj, 2005).

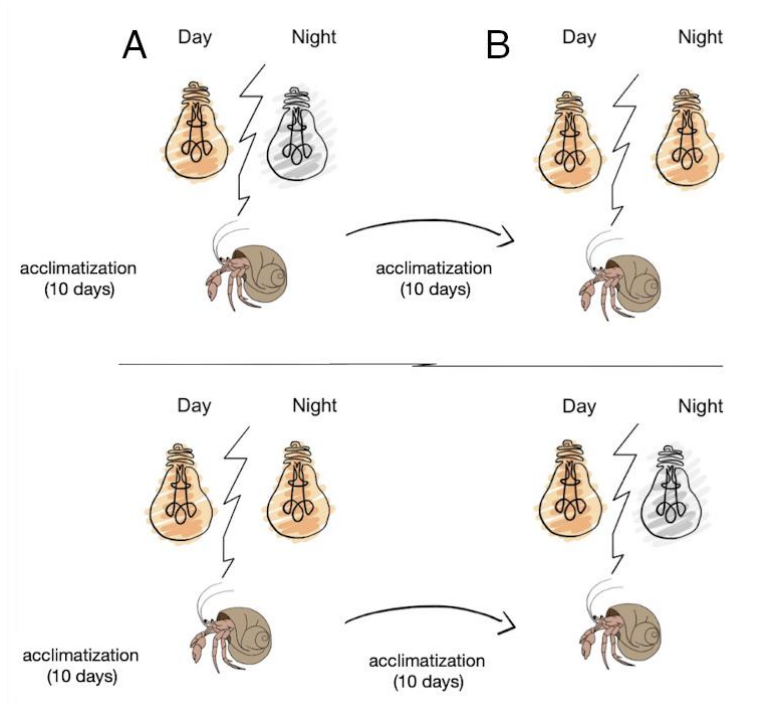


Figure 1: Schematic representation of the experiment's timeline, showing the experimental groups (constant and standard light) and the experimental crossover design. Incandescent light bulbs are used for illustrative purposes only, experiment was conducted using fluorescent light bulbs.

Metabolic rate measurements

To investigate whether metabolic rate varies in response to the light conditions, we measured the routine metabolic rate (routine MR) of 10 individuals in each group (constant light-A, N= 5; constant light-B, N= 5, standard light-A, N= 5; standard light-B, N= 5) exposed to the same conditions as described above. Routine MR was measured with a different cohort as startle response duration. Routine MR refers to an animal's average rate of metabolism and is measured when the animal is undergoing normal behaviours or some other specified type of activity (Dupont-Prinet et al., 2010; Speakman, 2013)

Animals used to estimate the routine MR were submitted to similar light conditions to those used in the behavioural assay. Thus, we measured each hermit crab's metabolic rate in two light regimes, constant and standard light. To minimise measurement errors, we measured routine MR with a different cohort of animals in the same room (i.e. same experimental conditions) where the animal was maintained and in parallel with the startle response duration. To ensure that changes in oxygen consumption were mediated by changes in light regime (i.e. standard or constant light treatment) and not a temporal component (i.e. duration of the

experiment, time in the laboratory), we performed MR measurements on alternating days on each condition.

We measured routine MR throughout 24 hours using the oxygen uptake as a proxy in a closed chamber respirometer. Due to experimental limitations, we only measured one hermit crab at a time (20 measurements in total). We used an oxygen-sensitive sensor spot (PreSens Precision Sensing GmbH, Regensburg, Germany) attached to the inner wall of the chamber with a silicone rubber compound, as specified by the manufacturer. This approach allowed non-invasive and more precise measures by preventing gas exchange during the readings.

Measures conducted in closed chambers are never constant due to the continuous oxygen consumption by the animal. We used the difference in oxygen concentration over time to estimate the oxygen consumption inside the chamber, which can be read by the sensor spot and recorded by a Fibox 4 trace machine (PreSens Precision Sensing GmbH, Regensburg, Germany) attached to a temperature sensor (Pt100, Bioengineering AG, Wald, Switzerland). To prevent oxygen stratification and ensure enough water mixing, we placed the chamber onto a multi-channel magnetic stirrer (MIX 15 eco; 2mag A.G., Munich, Germany) with a magnetic flea inside. We placed a mesh between the hermit crab and the magnetic flea to prevent contact between them.

We sealed the chambers underwater using filtered seawater to prevent air bubbles and minimise bacterial and algal activity. As a preventive measure against algal or bacterial activity, we also measured the oxygen consumption in three extra chambers ('blanks') containing a single *L. littorea* shell of a similar size as used by the crab. Differences in oxygen concentration in the blanks indicated microbial activity and were accounted for during routine MR estimation of *P. bernhardus*. We obtained the O₂ consumption rate using the slope of a linear regression of the oxygen consumption over time minus the blank O₂ consumption rate (Calosi et al., 2013). Then, we multiplied the slope by the oxygen solubility coefficient and adjusted for salinity and temperature. Although we conducted the metabolic rate measurements in a temperature-controlled room, there were minimal fluctuations in temperature (0.2 - 1°C), which can affect oxygen solubility values (Calosi et al., 2013; Widdows et al., 2002). We accounted for such minor changes in temperature in estimating the oxygen solubility coefficient (as described above). We calculate the rate of O₂ consumption using:

$$Rate\ of\ O_2\ uptake\ (\mu moles\ O_2 h^{-1}) = C(t) \times (V_r) \times \left(\frac{60}{t_1 - t_2} \right)$$

Where C(t) is the O₂ consumption rate (from the linear regression of oxygen consumption over time), V_r is the total volume of water inside the jar (jar volume minus the hermit crab volume), and t₁-t₂, is the measurement period (in minutes; (Calosi et al., 2013; Widdows et al., 2002). To estimate the metabolic rate and create a standardised measure, allowing comparisons between individuals, we divided the rate of O₂ uptake by individual body mass (Porter and Brand, 1995). We allowed hermit crabs to rest for 30 minutes before starting routine MR measures of oxygen consumption. We kept the same individual during the 24 hours' measurement to prevent stress

and possible disturbances in the animal. Although the metabolic rate was estimated during 24h continuous measurement, it was later divided into two experimental blocks, corresponding to day and night-time measures (12 - 12 h). Oxygen levels were carefully monitored throughout the experiment, and if oxygen concentration dropped below a threshold, the investigation would be interrupted and restarted with a different hermit crab. However, this step was not necessary.

Haemocyanin concentration

After completing the behavioural observations, we extracted a haemolymph sample from hermit crabs from both metabolic rate measurement and startle response duration (standard light; N = 20 and constant light; N = 20), following the protocol described by Bridger et al. (Bridger et al., 2015) by inserting an insulin syringe into the infra-branchial sinus. Then, we transferred 10µl of the haemocyanin recently sampled into a semi-micro cuvette containing 690 µl of double-distilled water. After mixing, we measured the haemocyanin absorbance at 337 nm in a spectrophotometer. We used the Nickerson & Van Holder (1971) extinction coefficient to determine the haemocyanin concentration. After the haemolymph collection, we euthanised all individuals by placing them into a saturated magnesium chloride solution.

Data analysis

We used three analyses to investigate the effect of constant light on the startle response. In the first analysis, we quantified the impact of light and dark conditions on the duration of the startle response using a hierarchical generalised linear model (HGLM) implemented within a Bayesian framework (MCMC Bayesian approach implemented in the R package MCMCglmm; Hadfield, 2010). We then used a second HGLM to estimate treatment group and time-specific repeatabilities (these could not be obtained from the primary model used to test for mean level effects; see details below). In the third analysis, we determined the impact of constant light on metabolic rate using repeated-measures ANOVA. Analysis, results and raw data can be viewed at <https://github.com/marivelasque/Light-pollution>.

Personality and behavioural variation

In the first analysis, we fitted a model allowing a random intercept for each individual. This enables the estimation of between-individual variation in startle responses (V_{BI} : between-individual variance) and random slopes across the repeated observations (V_{WI} : within-individual or residual variance, providing a measure of consistency) and the estimation of individual variation across all observations. To account for the time the animal was in the laboratory, we added the experimental period as a random effect. We assumed the residual variance to be normally distributed and uncorrelated across all observations. We used the startle response duration (\log_{10} transformed to improve normality) as the response variable and time at which startle response duration was measured (day or night), treatment (constant or standard light),

occasion (day 1-20) on which the behaviour was observed, the hermit crab mass, the haemocyanin concentration as fixed effects. Because startle response duration is likely to vary according to the time of the day on which it was measured and the experimental treatment. We also included the interactions between treatment * time as fixed effects.

To compare repeatability (and V_{BI} and V_{WI} components) across treatment groups, we modelled another HGLM with a similar structure for fixed effects as the model described above. To achieve this, we constructed a model using block-specific (i.e. treatment groups) random intercepts for individuals, on which the within-group covariance was constrained to 0 and the within-group (diagonals) were allowed to vary (i.e. measures within each light treatment and time of the day were allowed to vary), creating a block-specific G-structure that corresponds to V_{BI} . Similar to the previous model, we also compared effect size, autocorrelation between estimated samples and DIC of this model against five priors (see Supplemental Material S1) to choose the best-unbiased model based on the overall results. We report the results obtained using 'prior 2' as it achieved convergence and had lower autocorrelation between samples (see Supplemental Material S1). All models had similar DIC values. We reported the posterior mode for fixed effects and 95% credible intervals (C.I.s). Additionally, we modelled separate residual variances for each experimental block (R-structure, corresponding to V_{WI}).

We estimated the posterior modes for repeatability in each experimental block (with 95% C.I.s). We also determined whether the repeatability estimates showed significant differences among the experimental blocks by calculating the posterior modal differences between blocks (ΔR ; see Supplemental Material S1) and the 95% CI values of these differences (Osborn and Briffa, 2017; Royauté et al., 2015; White and Briffa, 2017). We estimated the difference in repeatability, ΔR , between treatments within each time of day ($R_{\text{constant light}} - R_{\text{standard light}}$) and between each time of day within groups ($R_{\text{constant light during day}} - R_{\text{constant light during night}}$; $R_{\text{standard light during day}} - R_{\text{constant light during night}}$). We made similar calculations to assess the changes in the specific variance components of repeatability (ΔV_{BI} and ΔV_{WI}) between treatments and times of the day.

In all Bayesian modules, we compared the effect size, autocorrelation between estimated samples and Deviance Information Criterion (DIC) with four different priors to choose the best-unbiased model based on the overall results (see Supplemental Material S1). We report the results obtained using the model containing the lower autocorrelation between samples (see Supplemental Material S1). All models had similar DIC values. As standard when implementing Bayesian framework, significance occurs when 95% C.I.s of their posterior modes did not overlap zero. We specified a Markov Chain Monte Carlo (MCMC) for both models with 5×10^6 interactions, a thinning interval of 100 and a burn-in of 50000. We fitted all models using MCMC methods (implemented with MCMCglmm in R version 3.6.0).

The effect of constant light on metabolic rate and haemocyanin concentration

In the third analysis, we determined the effect of light on metabolic rate using a Linear Mixed-Effects Model. As the metabolic data was not normally distributed, we applied Log10 +1

transformation before analysis. We used metabolic rate as the dependent variable and added it as a fixed effect containing the time of the day and an interaction between the treatment group and experiment period (i.e. crossover). To account for the crossover effect, we built a model containing a random intercept (i.e. individuals) and random slopes (i.e. experimental period), indicating that individual slopes vary across different experimental periods). This analysis was performed using the lmer function from the lme4 package on R. As haemocyanin was only measured once at the end of the experiment, we also tested the effect of treatment on its concentration using Welch's t-test (Lu and Yuan, 2010).

Results

Personality and behavioural variation

The parameter estimates for both random and fixed effects of the HGML model and their 95% credible intervals (and estimated p values) are given in Table 1. The fixed effects components of the HGLM model provide strong evidence that the startle response duration changed according to the treatment ($p < 0.001$), being longer in animals experiencing the constant light treatment (Figure 2). We also found strong support that startles response duration did not vary between day and night measures ($p = 0.87$) nor with the hermit crab mass ($p = 0.065$).

Although we did not find a significant change in startle response behaviour between day and night-time measures, we found strong evidence that boldness changed with the interaction between treatment and time ($p < 0.001$; Figure 2; Table 1). Our results suggest that the difference in startle response duration between day and night was more marked for the constant light than standard light treatment ($p < 0.001$; Figure 2; Table 1). In addition, we found strong evidence that the decrease in boldness was greater in hermit crabs with higher haemocyanin concentration ($p < 0.01$; Figure 2; Table 1). Startle response duration also decreased throughout the experiment ($p = 0.036$; Table 1). We estimated the repeatability from the second HGLM (see Supplemental Material S1). The repeatability estimates (Table 2) provide strong evidence that the startle response duration was repeatable in all treatment blocks. There was no significant difference in repeatability between treatment groups within periods. The HGLM model also indicates an increased amount of variation in response to changes in light conditions, both between (V_{BI-}) and within-individuals (V_{Wi} ; Table 3). It also indicates that such response was consistent across individuals (V_{BI}) in different experimental groups and times of the day. Although such behavioural consistency was considerable throughout the experimental group, individuals on the standard light treatment had a lower behavioural consistency during the day.

The effect of constant light on metabolic rate and haemocyanin concentration

In addition to behavioural changes, hermit crabs exposed to constant light also had significantly higher MR than those in standard light conditions. ($p = 0.001$, Figure 2; Table 4). We also found the metabolic rate to vary with the period, being higher during the second part of the experiment ($p = 0.043$; Table 4). In addition, we also found that such crossover effect was significantly

367 higher when animals were exposed to constant light in the second experimental period instead of
368 the first (Treatment x Period - $p = 0.008$; Table 4). We did not find any changes in metabolic rate
369 between day and night-time measures ($p = 0.509$; Table 4). We also found that constant light
370 significantly increases haemocyanin concentration in hermit crabs ($t_{17.401} = -3.173$, $p = 0.005$).

371 Table 1: Posterior summary statistics for the mean effect of startle response, showing posterior
 372 mean, lower and upper 95% C.I.s and P-values (for fixed effect only). Significant values are
 373 shown in bold.

Parameter name	Posterior mean	95% CI lower	95% CI Upper	<i>p</i>
Fixed effects				
Intercept	-29.262	-3.3272	7.1733	0.12
Time	0.0134	-0.1647	0.2084	0.87
Treatment	0.573	0.3925	0.7685	< 0.001
Occasion	0.0248	0.0023	0.048	0.036
Mass	-0.2503	-0.5195	-3e-04	0.065
Haemocyanin concentration	0.0073	0.0041	0.0109	< 0.001
Treatment x Time	-0.7164	-0.9748	-0.4443	< 0.001
Random intercepts (between-individual variation, G-structure and R-structure)				
Hermit Crab ID (intercept)	9e-04	4e-04	0.0013	-
Observational period	1534349.5381	4e-04	95.2922	-
Error	1.1287	0.9702	1.2785	-

375 Table 2: Posterior modes, upper and lower 95% C.I.s (in brackets) for MCMC repeatability
 376 estimates between treatment groups within periods and repeatability of differences (Δ) between
 377 treatments ($\Delta_{\text{constant light - standard light}}$) and between the time on which the startle response was
 378 induced ($\Delta_{\text{Night-Day}}$). Significant values are shown in bold.

	Day	Night	$\Delta_{\text{Night-Day}}$
constant light	0.34 [0.248, 0.535]	0.23 [0.127, 0.374]	0.15 [-0.043, 0.347]
standard light	0.49 [0.358, 0.65]	0.35 [0.22, 0.503]	0.14 [-0.078, 0.332]
$\Delta_{\text{constant - standard light}}$	-0.12 [-0.313, 0.109]	-0.11 [-0.311, 0.073]	-

379

Table 3: Posterior modes, upper and lower 95% C.I.s (in brackets) for (a) between and (b) within-individual variation in startle response duration between treatment groups within periods and the difference (Δ) in variation between treatments ($\Delta_{\text{constant light - standard light}}$) and between the time on which the startle response was induced ($\Delta_{\text{Night-Day}}$). Significant values are shown in bold

(a) Between-individual variation, V_{BI}

	Day	Night	$\Delta_{\text{Night-Day}}$
constant light	0.55 [0.278, 0.977]	0.30 [0.139, 0.541]	0.26 [-0.131, 0.745]
standard light	0.71 [0.377, 1.249]	0.56 [0.288, 0.993]	0.22 [-0.461, 0.785]
$\Delta_{\text{constant light - standard light}}$ in VBI	-0.04 [-0.797, 0.416]	-0.23 [-0.733, 0.167]	-

(b) Within-individual variation, V_{WI}

	Day	Night	$\Delta_{\text{B-A}}$
constant light	0.94 [0.77, 1.05]	0.97 [0.79, 1.11]	0.06 [-0.18, 0.24]
standard light	0.73 [0.63, 0.89]	1.03 [0.85, 1.21]	0.29 [0.04, 0.48]
$\Delta_{\text{constant light - standard light}}$	-0.13 [-0.81, 0.51]	-0.11 [-0.31, 0.16]	-

Table 4: Fixed-effects estimates for the Linear Mixed-Effects Models for the effect of time (day or night-time), experimental period (crossover A or B) and treatment group (constant light or standard light) on metabolic rate of hermit crabs. Significant values are shown in bold.

	Estimate	Std. Error	df	t-value	Pr(> z)
Intercept	0.477	0.166	19.559	2.87	0.01
Treatment	0.977	0.235	19.559	4.159	0.001
Period	0.52	0.245	26.801	2.122	0.043
Time	-0.142	0.212	23.999	-0.67	0.509
Treatment x Period	-1.177	0.386	15.399	-3.047	0.008
Treatment x Time	-0.395	0.299	23.999	-1.319	0.2
Period x Time	0.103	0.299	23.999	0.344	0.734
Treatment x Period x Time	0.627	0.423	23.999	1.482	0.151

Reference values: Treatment – constant light; Period – B; Time - night.

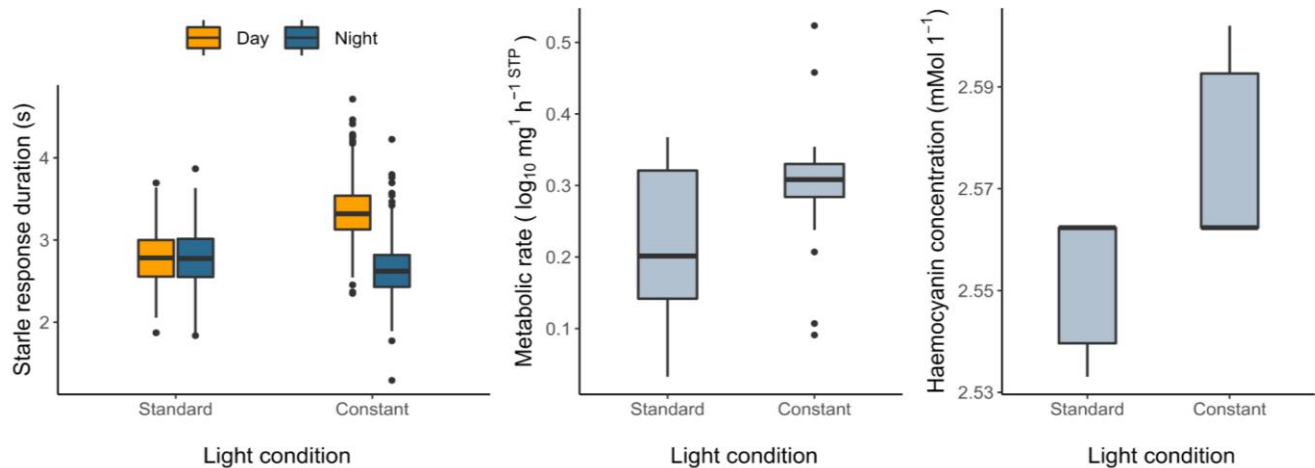


Figure 2. Night-time light and time effects on the startle response duration, metabolic rate, and haemocyanin concentration of the hermit crab *Pagurus bernhardus*. A) Startle response duration was predicted using the best unbiased HGLM model (see materials and methods). B) the metabolic rate (MO₂). *Pagurus bernhardus*. Metabolic rate is expressed as log₁₀ nmol O₂ mg⁻¹ h⁻¹ STP (STP - standard temperature and pressure) and haemocyanin concentration as mMol l⁻¹.

397 Discussion & Conclusions

398 We investigated the effect of constant light on personality traits and metabolic rate in the hermit
399 crab *Pagurus bernhardus*. We show that night-time light influences mean level startle response
400 durations and repeatability estimates. Although startle responses observed during the night were
401 unaffected, those individuals kept under constant light exhibited reduced boldness during day-
402 time hours (with longer startle response duration) than individuals experiencing standard light
403 conditions. Our data also indicates that animals kept under constant light conditions showed a
404 higher metabolic rate than those under standard light conditions. The increased haemocyanin
405 concentration in constant light treated animals indicates an increased oxygen demand resulting
406 from an increased metabolic rate.

407 Night-time light increases animal visibility facilitating predator detection, and thus,
408 increases perceived predation risk (Prugh and Golden, 2014; Troscianko et al., 2009). Previous
409 studies in *P. bernhardus* have shown that hermit crabs can be aware of the shell conspicuousness
410 and predation risk associated with the shell and in turn displayed a modified startle response
411 duration (Briffa and Twyman, 2011). However, we found no overall significant difference in
412 startle response duration between day and night measures. Nevertheless, this effect depends on
413 the treatment. Hermit crabs experiencing constant light had shorter startle response duration at
414 night-time than individuals under standard light regimes. This suggests that constant light
415 treatment may increase hermit crab conspicuousness and, consequently, the perceived risk
416 (Gaston and Spicer, 2013). However, *P. bernhardus* is less active at night (Mitchell, 1973), such
417 perceived risk may be transferred, causing more severe behavioural changes when hermit crabs
418 are more active (i.e. day). Perhaps long-term adaptation may result in increased activity during
419 the daytime, but this was not observed in this work. It is also possible that constant light disrupts
420 resting and sleep behaviour (Alaasam et al., 2021; Jiang et al., 2020; Raap et al., 2016b) in
421 hermit crabs, increasing stress and modifying activity patterns and response to risk.

422 Startle response duration is a complex behaviour widely used as a proxy for defensive
423 response in several animals. In hermit crabs, gas exchange occurs in modified gills located in the
424 brachial chamber (Gerlach et al., 1976; Lancaster, 1990). When they withdraw inside their shells,
425 such gas exchange is interrupted, temporarily limiting oxygen availability. Hence, the increase in
426 startle response duration will cause a reduction in oxygen availability, creating a trade-off (Briffa
427 and Bibost, 2009). Traits with a substantial trade-off tend to vary both in populations and
428 throughout an organism's lifetime (i.e. shorter to long). Traits with inter- and intra-individual
429 variation are an important coping strategy, as they reduce the ability of predators to adapt to prey
430 behaviour (Briffa, 2013; Briffa et al., 2013). Although we found that hermit crabs adapt their
431 average day-time behaviour in response to constant light (i.e. decreasing boldness), there were no
432 differences in predictability (i.e. V_{WI}) between light treatments. Constant light did, however, lead
433 to an increase in energy consumption (when compared with standard light regimes). Therefore, it
434 is possible that under long-term constant light, hermit crabs need to increase their food
435 consumption to support their high energetic demand (Lima, 1998; Lima and Dill, 1990) which

increases foraging and, therefore, the predation risk (Lima, 1998; Lima and Dill, 1990). Animals in captivity tend to have a more homogeneous behaviour due to reduced environmental heterogeneity (Bell et al., 2009; Dammhahn and Almeling, 2012; Desy et al., 1990). However, captive animals still have some activity pattern with higher and lower activity phases, usually reinforced by light (e.g. circadian rhythms: (Palmer, 1973). Thus, under constant light conditions, such patterns are expected to be minimised (Ringelberg, 2007; Wyse et al., 2011), producing a more homogeneous response (e.g. lower variance or higher repeatability). However, we found no evidence for this, with constant light exposed individuals similar to those under the standard light and dark regime. The repeatability within groups (i.e., consistent behavioural differences among individuals the day versus night) was also similar across treatment groups.

Individuals in both treatment groups and at both periods exhibit significant between- and within-individual variance in boldness (V_{BI} and V_{WI} , respectively). There was also no significant variation in V_{BI} between treatment groups and time. However, under standard light and dark regime treatment, there was a substantial difference in the amount of within-individual variation (V_{WI}) between day and night; crabs had more within-individual variation in behaviour (less consistent) at night than during the day (Table 3). One possible explanation is that *P. bernhardus* is a diurnal species, maintaining its activity pattern even under constant light (Mitchell, 1973). Therefore, it is possible that in the absence of constant light exposure, other rhythms than circadian (tidal or lunar) are more pronounced, resulting in a higher variation in behaviour within-individuals. Alternatively, hermit crabs may be subjected to different pressures throughout a 24-hour period. For instance, the predation risk increases during the night-time and thus, decreasing predictability (increases V_{WI}) may increase survival in natural conditions. Therefore low predictability (i.e. low behavioural consistency or high V_{WI}), alongside low boldness, is potentially a strategy to cope with risk, as less predictable individuals might reduce the chance of being captured (Briffa, 2013; Briffa et al., 2013).

How organisms respond to ALAN is not homogeneous and varies across species, seasons and even daily activity patterns. For instance, some animals showed a significant decrease in energy expenditure (Duarte et al., 2019; Manríquez et al., 2019; Pulgar et al., 2019; Touzot et al., 2019). The usage of the crossover design allowed us to test the effect of the treatment while avoiding confounding factors, such as time and habituation (Briffa, 2013; Briffa et al., 2008; Briffa and Bibost, 2009; Briffa and Twyman, 2011; Mowles et al., 2012).

Light pollution is a modern, globally widespread (Cinzano et al., 2001) and fast-expanding (Hölker et al., 2010) issue. Nevertheless, the effect on marine life is not well documented, especially for invertebrates. To our knowledge, no prior studies have explored the effects of constant light as a potential driver (or disruptor) of variation in repeatable personality traits. Previous work examining ALAN induced personality changes in guppies did not appear to influence variation (Kurvers et al., 2018). Therefore, our study shows how light pollution may affect *P. bernhardus* physiologically, increasing metabolic rate and behaviourally by reducing within-individual variation in behaviour and decreasing boldness overall. Further experiments are required to explore the potential downstream effects of these light pollution-induced changes.

For instance, it has been shown that hermit crabs exposed to predator chemical cues (e.g. effluent form containers with a predator) or visual (e.g. predator model) cues tend to adjust their behaviour (Briffa, 2013; Briffa et al., 2008) and could be used to simulate risk under varying light treatments. Our results (increased metabolic rate and decreased day-time boldness), indicate that artificial light at night can cause systemic changes to hermit crab's physiology and risk coping mechanisms. Furthermore, such changes in response to light conditions could interact potentially in a non-linear way. If elevated metabolism requires greater foraging, under elevated predation risk, then increased foraging behaviour could place crabs under even greater risk. On the other hand, if crabs try to avoid elevated predation risk by foraging less, their energy balance will be negatively impacted under conditions of increased metabolic rate. We did not measure foraging in this experiment, but since boldness is linked to the exploration in hermit crabs (Mowles and Briffa, 2012), the second of these two scenarios seem the most likely. Such changes could influence individual fitness and population stability in affected areas.

Acknowledgements

The work leading to this publication was part of a PhD scholarship awarded to MV funded by Coordination for the Improvement of Higher Education- Brazil (CAPES), Science Without Borders Program, CsF. We thank Marie Palmer, Richard Ticehurst and Ann Torr for technical assistance during fieldwork and animal husbandry.

Declaration of interests

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.

References

- Alaasam, V.J., Liu, X., Niu, Y., Habibian, J.S., Pieraut, S., Ferguson, B.S., Zhang, Y., Ouyang, J.Q., 2021. Effects of dim artificial light at night on locomotor activity, cardiovascular physiology, and circadian clock genes in a diurnal songbird. *Environ. Pollut.* 282, 117036. <https://doi.org/10.1016/j.envpol.2021.117036>
- Amadi, N., Luiselli, L., Belema, R., Nyiwale, G.A., Wala, C., Urubia, N., Meek, R., 2021. From diurnal to nocturnal activity: a case study of night-light niche expansion in *Agama agama* lizards. *Ethology Ecology & Evolution*. <https://doi.org/10.1080/03949370.2021.1883120>
- Ayalon, I., Rosenberg, Y., Benichou, J.I.C., Campos, C.L.D., Sayco, S.L.G., Nada, M.A.L., Baquiran, J.I.P., Ligson, C.A., Avisar, D., Conaco, C., Kuechly, H.U., Kyba, C.C.M., Cabaitan, P.C., Levy, O., 2021. Coral Gametogenesis Collapse under Artificial Light Pollution. *Curr. Biol.* 31, 413-419.e3. <https://doi.org/10.1016/j.cub.2020.10.039>
- Baskir, E.A., Hazen, R.E., Powell, D.M., 2021. Documenting nocturnal activity of dragon-headed katydids (*Lesina blanchardi*) under artificial light. *Zoo Biology*. <https://doi.org/10.1002/zoo.21608>
- Belgrad, B.A., Karan, J., Griffen, B.D., 2017. Individual personality associated with interactions between physiological condition and the environment. *Anim. Behav.* 123, 277–284.

- <https://doi.org/10.1016/j.anbehav.2016.11.008>
- Bell, A.M., Hankison, S.J., Laskowski, K.L., 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Benedict, J.E., 1901. The hermit crabs of the *Pagurus bernhardus* type. *Proceedings of the United States National Museum*. <https://doi.org/10.5479/si.00963801.23-1216.451>
- Bennie, J., Davies, T.W., Cruse, D., Inger, R., Gaston, K.J., 2018. Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. *J. Appl. Ecol.* 55, 2698–2706. <https://doi.org/10.1111/1365-2664.13240>
- Bergmüller, R., 2010. Animal personality and behavioural syndromes, in: *Animal Behaviour: Evolution and Mechanisms*. pp. 587–621. https://doi.org/10.1007/978-3-642-02624-9_19
- Bevan, P.A., Gosetto, I., Jenkins, E.R., Barnes, I., Ioannou, C.C., 2018. Regulation between personality traits: individual social tendencies modulate whether boldness and leadership are correlated. *Proc. Biol. Sci.* 285. <https://doi.org/10.1098/rspb.2018.0829>
- Biro, P.A., Abrahams, M.V., Post, J.R., Parkinson, E.A., 2006. Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *J. Anim. Ecol.* 75, 1165–1171. <https://doi.org/10.1111/j.1365-2656.2006.01137.x>
- Botha, L.M., Michael Botha, L., Jones, T.M., Hopkins, G.R., 2017. Effects of lifetime exposure to artificial light at night on cricket (*Teleogryllus commodus*) courtship and mating behaviour. *Animal Behaviour*. <https://doi.org/10.1016/j.anbehav.2017.05.020>
- Bridger, D., Bonner, S.J., Briffa, M., 2015. Individual quality and personality: bolder males are less fecund in the hermit crab *Pagurus bernhardus*. *Proc. Biol. Sci.* 282, 20142492. <https://doi.org/10.1098/rspb.2014.2492>
- Briffa, M., 2013. Plastic proteans: reduced predictability in the face of predation risk in hermit crabs. *Biol. Lett.* 9, 20130592. <https://doi.org/10.1098/rsbl.2013.0592>
- Briffa, M., Bibost, A.-L., 2009. Effects of shell size on behavioural consistency and flexibility in hermit crabs. *Can. J. Zool.* 87, 597–603. <https://doi.org/10.1139/Z09-047>
- Briffa, M., Bridger, D., Biro, P.A., 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Anim. Behav.* 86, 47–54. <https://doi.org/10.1016/j.anbehav.2013.04.009>
- Briffa, M., Elwood, R.W., 2007. Monoamines and decision making during contests in the hermit crab *Pagurus bernhardus*. *Anim. Behav.* 73, 605–612.
- Briffa, M., Rundle, S.D., Fryer, A., 2008. Comparing the strength of behavioural plasticity and consistency across situations: animal personalities in the hermit crab *Pagurus bernhardus*. *Proc. Biol. Sci.* 275, 1305–1311. <https://doi.org/10.1098/rspb.2008.0025>
- Briffa, M., Twyman, C., 2011. Do I stand out or blend in? Conspicuousness awareness and consistent behavioural differences in hermit crabs. *Biol. Lett.* 7, 330–332. <https://doi.org/10.1098/rsbl.2010.0761>
- Briffa, M., Weiss, A., 2010. Animal personality. *Current Biology*. <https://doi.org/10.1016/j.cub.2010.09.019>
- Brisbane, J.L.K., van den Burg, M.P., 2020. No need for artificial light: nocturnal activity by a diurnal reptile under lunar light. *Neotropical Biodiversity*. <https://doi.org/10.1080/23766808.2020.1844993>
- Bubac, C.M., Coltman, D.W., Don Bowen, W., Lidgard, D.C., Lang, S.L.C., den Heyer, C.E., 2018. Repeatability and reproductive consequences of boldness in female gray seals. *Behav. Ecol. Sociobiol.* 72, 527. <https://doi.org/10.1007/s00265-018-2515-5>
- Burgess, S.C., Marshall, D.J., 2014. Adaptive parental effects: the importance of estimating

- environmental predictability and offspring fitness appropriately. *Oikos*.
<https://doi.org/10.1111/oik.01235>
- Calosi, P., Turner, L.M., Hawkins, M., Bertolini, C., Nightingale, G., Truebano, M., Spicer, J.I.,
 2013. Multiple physiological responses to multiple environmental challenges: an
 individual approach. *Integr. Comp. Biol.* 53, 660–670. <https://doi.org/10.1093/icb/ict041>
- Careau, V., Thomas, D., Humphries, M.M., Réale, D., 2008. Energy metabolism and animal
 personality. *Oikos*. <https://doi.org/10.1111/j.0030-1299.2008.16513.x>
- Carter, A.J., Feeney, W.E., Marshall, H.H., Cowlshaw, G., Heinsohn, R., 2013. Animal
 personality: what are behavioural ecologists measuring? *Biological Reviews* 88, 465–
 475. <https://doi.org/10.1111/brv.12007>
- Cinzano, P., Falchi, F., Elvidge, C.D., 2001. The first World Atlas of the artificial night sky
 brightness. *Monthly Notices of the Royal Astronomical Society*.
<https://doi.org/10.1046/j.1365-8711.2001.04882.x>
- Dammhahn, M., Almeling, L., 2012. Is risk taking during foraging a personality trait? A field
 test for cross-context consistency in boldness. *Anim. Behav.* 84, 1131–1139.
<https://doi.org/10.1016/j.anbehav.2012.08.014>
- Dammhahn, M., Dingemanse, N.J., Niemelä, P.T., Réale, D., 2018. Pace-of-life syndromes: a
 framework for the adaptive integration of behaviour, physiology and life history. *Behav.*
Ecol. Sociobiol. 72, 62. <https://doi.org/10.1007/s00265-018-2473-y>
- 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? *Glob.*
Chang. Biol. 19, 1417–1423. <https://doi.org/10.1111/gcb.12166>
- Davies, T.W., Duffy, J.P., Bennie, J., Gaston, K.J., 2014. The nature , extent , and ecological
 implications of marine light pollution. *Front. Ecol. Environ.* 12, 347–355.
<https://doi.org/10.1890/130281>
- Degen, T., 2015. Female Mating Success Under Altered Sex-specific Mortality and Various
 Male and Female Encounter Rates: Does Artificial Light at Night Force Evolution?
- Desy, E. a., Batzli, G.O., Liu, J., 1990. Effects of food and predation on behaviour of prairie
 voles : a field experiment. *Oikos* 58, 159–168. <https://doi.org/10.2307/3545423>
- Dickerson, A.L., Hall, M.L., Jones, T.M., 2022. The effect of natural and artificial light at night
 on nocturnal song in the diurnal willie wagtail. *Sci. Total Environ.* 808, 151986.
<https://doi.org/10.1016/j.scitotenv.2021.151986>
- Dingemanse, N.J., Kazem, A.J.N., Réale, D., Wright, J., 2010. Behavioural reaction norms:
 animal personality meets individual plasticity. *Trends Ecol. Evol.* 25, 81–89.
<https://doi.org/10.1016/j.tree.2009.07.013>
- Duarte, C., Quintanilla-Ahumada, D., Anguita, C., Manríquez, P.H., Widdicombe, S., Pulgar, J.,
 Silva-Rodríguez, E.A., Miranda, C., Manríquez, K., Quijón, P.A., 2019. Artificial light
 pollution at night (ALAN) disrupts the distribution and circadian rhythm of a sandy
 beach isopod. *Environ. Pollut.* 248, 565–573.
<https://doi.org/10.1016/j.envpol.2019.02.037>
- Dupont-Prinet, A., Chatain, B., Grima, L., Vandeputte, M., Claireaux, G., McKenzie, D.J., 2010.
 Physiological mechanisms underlying a trade-off between growth rate and tolerance of
 feed deprivation in the European sea bass (*Dicentrarchus labrax*). *J. Exp. Biol.* 213,
 1143–1152.
- Elwood, R.W., n.d. Hermit Crabs – Information Gathering by the Hermit Crab, *Pagurus*
bernhardus. *Field and Laboratory Methods in Animal Cognition*.

- <https://doi.org/10.1017/9781108333191.012>
- Farnworth, B., Innes, J., Kelly, C., Littler, R., Waas, J.R., 2018. Photons and foraging: Artificial light at night generates avoidance behaviour in male, but not female, New Zealand weta. *Environmental Pollution*. <https://doi.org/10.1016/j.envpol.2018.01.039>
- Finch, D., Smith, B.R., Marshall, C., Coomber, F.G., Kubasiewicz, L.M., Anderson, M., Wright, P.G.R., Mathews, F., 2020. Effects of Artificial Light at Night (ALAN) on European Hedgehog Activity at Supplementary Feeding Stations. *Animals (Basel)* 10. <https://doi.org/10.3390/ani10050768>
- Finstad, A.G., Forseth, T., Ugedal, O., Næsje, T.F., 2007. Metabolic rate, behaviour and winter performance in juvenile Atlantic salmon. *Functional Ecology*. <https://doi.org/10.1111/j.1365-2435.2007.01291.x>
- Forsburg, Z.R., Guzman, A., Gabor, C.R., 2021. Artificial light at night (ALAN) affects the stress physiology but not the behavior or growth of *Rana berlandieri* and *Bufo valliceps*. *Environ. Pollut.* 277, 116775. <https://doi.org/10.1016/j.envpol.2021.116775>
- Galliard, J., Paquet, M., Cisel, M., Montes-Poloni, L., 2013. Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Funct. Ecol.* 27, 136–144.
- Galliard, J.-F.L., Le Galliard, J.-F., Paquet, M., Cisel, M., Montes-Poloni, L., 2013. Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.12017>
- Gasparini, C., Speechley, E.M., Polverino, G., 2019. The bold and the sperm: positive association between boldness and sperm number in the guppy. *Royal Society Open Science* 6, 190474. <https://doi.org/10.1098/rsos.190474>
- Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol. Rev. Camb. Philos. Soc.* 88, 912–927. <https://doi.org/10.1111/brv.12036>
- Gaston, K.J., Spicer, J.I., 2013. *Biodiversity: An Introduction*. John Wiley & Sons.
- Gerlach, S.A., Ekstrøm, D.K., Eckardt, P.B., 1976. Filter feeding in the hermit crab : *Pagurus bernhardus*. *Oecologia* 24, 257–264. <https://doi.org/10.1007/BF00345477>
- Hadfield, J.D., 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Softw.* 33, 1–22. <https://doi.org/10.1002/ana.22635>
- Hazlett, B.A., 1966. Social behavior of the Paguridae and Diogenidae of Curacao. *Studies on the Fauna of Curaçao and other Caribbean Islands* 23, 1–143.
- Hillyer, K.E., Beale, D.J., Shima, J.S., 2021. Artificial light at night interacts with predatory threat to alter reef fish metabolite profiles. *Sci. Total Environ.* 769, 144482. <https://doi.org/10.1016/j.scitotenv.2020.144482>
- Hölker, F., Wolter, C., Perkin, E.K., Tockner, K., 2010. Light pollution as a biodiversity threat. *Trends Ecol. Evol.* 25, 681–682.
- Holtmann, B., Lagisz, M., Nakagawa, S., 2017. Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: a meta-analysis. *Funct. Ecol.* 31, 685–696. <https://doi.org/10.1111/1365-2435.12779>
- Hut, R.A., Beersma, D.G.M., 2011. Evolution of time-keeping mechanisms: early emergence and adaptation to photoperiod. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 366, 2141–2154. <https://doi.org/10.1098/rstb.2010.0409>
- Jiang, J., He, Y., Kou, H., Ju, Z., Gao, X., Zhao, H., 2020. The effects of artificial light at night on Eurasian tree sparrow (*Passer montanus*): Behavioral rhythm disruption, melatonin

suppression and intestinal microbiota alterations. *Ecol. Indic.* 108, 105702.
<https://doi.org/10.1016/j.ecolind.2019.105702>
 Kurvers, R.H.J.M., Drägestein, J., Hölker, F., Jechow, A., Krause, J., Bierbach, D., 2018.
 Artificial Light at Night Affects Emergence from a Refuge and Space Use in Guppies.
Sci. Rep. 8, 14131. <https://doi.org/10.1038/s41598-018-32466-3>
 Lancaster, I.L.B.-. 2763, 1990. Reproduction and life history strategy of the hermit crab *Pagurus*
bernhardus. *Journal of Marine Biology Assessment* 70, 129–142.
<https://doi.org/10.1017/S0025315400034251>
 Lantová, P., Zub, K., Koskela, E., Šichová, K., Borowski, Z., 2011. Is there a linkage between
 metabolism and personality in small mammals? The root vole (*Microtus oeconomus*)
 example. *Physiology & Behavior* 104, 378–383.
<https://doi.org/10.1016/j.physbeh.2011.04.017>
 Le Tallec, T., Perret, M., Théry, M., 2013. Light pollution modifies the expression of daily
 rhythms and behavior patterns in a nocturnal primate. *PLoS One* 8, e79250.
<https://doi.org/10.1371/journal.pone.0079250>
 Lima, S.L., 1998. Nonlethal Effects in the Ecology of Predator-Prey Interactions. *Bioscience* 48,
 25–34. <https://doi.org/10.2307/1313225>
 Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review
 and prospectus. *Can. J. Zool.* 68, 619–640. <https://doi.org/10.1139/z90-092>
 Lines, E.R., Zavala, M.A., Purves, D.W., Coomes, D.A., 2012. Predictable changes in
 aboveground allometry of trees along gradients of temperature, aridity and competition.
Global Ecology and Biogeography. <https://doi.org/10.1111/j.1466-8238.2011.00746.x>
 Lu, Z.L., Yuan, K.-H., 2010. Welch's t test. <https://doi.org/10.13140/RG.2.1.3057.9607>
 Duarte, T., Bonta, C.C., Silva-Rodriguez, E.A., Quijón, P.A., Miranda, C., Farias, A.A., Duarte,
 C., 2016. Light pollution reduces activity, food consumption and growth rates in a sandy
 beach invertebrate. *Environ. Pollut.* 218, 1147–1153.
<https://doi.org/10.1016/j.envpol.2016.08.068>
 Manríquez, P.H., Jara, M.E., Diaz, M.I., Quijón, P.A., Widdicombe, S., Pulgar, J., Manríquez,
 K., Quintanilla-Ahumada, D., Duarte, C., 2019. Artificial light pollution influences
 behavioral and physiological traits in a keystone predator species, *Concholepas*
concholepas. *Sci. Total Environ.* 661, 543–552.
<https://doi.org/10.1016/j.scitotenv.2019.01.157>
 Marangoni, L.F.B., Davies, T., Smyth, T., Rodríguez, A., Hamann, M., Duarte, C., Pendoley, K.,
 Berge, J., Maggi, E., Levy, O., 2022. Impacts of artificial light at night in marine
 ecosystems-A review. *Glob. Chang. Biol.* 28, 5346–5367.
<https://doi.org/10.1111/gcb.16264>
 Mitchell, K.A., 1973. Activities of two British species of *Pagurus* (Crustacea, Decapoda,
Paguroidea). *Mar. Freshw. Behav. Physiol.* 2, 229–236.
 Mowles, S.L., Briffa, M., 2012. Forewarned is forearmed: early signals of RHP predict opponent
 fatigue in hermit crab shell fights. *Behavioral Ecology* 23, 1324–1329.
<https://doi.org/10.1093/beheco/ars124>
 Mowles, S.L., Cotton, P.A., Briffa, M., 2012. Consistent crustaceans: The identification of stable
 behavioural syndromes in hermit crabs. *Behav. Ecol. Sociobiol.* 66, 1087–1094.
<https://doi.org/10.1007/s00265-012-1359-7>
 Naylor, E., 2010. *Chronobiology of Marine Organisms*. Cambridge University Press.
<https://doi.org/10.1017/cbo9780511803567>

- Nelson, R.J., 2019. Light at night influences neuroinflammation and metabolism. *Psychoneuroendocrinology*. <https://doi.org/10.1016/j.psyneuen.2018.12.198>
- Nickerson, K.W., Van Holde, K.E., 1971. A comparison of molluscan and arthropod hemocyanin—I. Circular dichroism and absorption spectra. *Comparative Biochemistry and Physiology Part B: Comparative Biochemistry* 39, 855–872. [https://doi.org/10.1016/0305-0491\(71\)90109-X](https://doi.org/10.1016/0305-0491(71)90109-X)
- O'Connor, J.J., Fobert, E.K., Besson, M., Jacob, H., Lecchini, D., 2019. Live fast, die young: Behavioural and physiological impacts of light pollution on a marine fish during larval recruitment. *Mar. Pollut. Bull.* 146, 908–914. <https://doi.org/10.1016/j.marpolbul.2019.05.038>
- Oosten, J.E., Magnhagen, C., Hemelrijk, C.K., 2010. Boldness by habituation and social interactions: a model. *Behav. Ecol. Sociobiol.* 64, 793–802. <https://doi.org/10.1007/s00265-009-0896-1>
- Osborn, A., Briffa, M., 2017. Does repeatable behaviour in the laboratory represent behaviour under natural conditions? A formal comparison in sea anemones. *Anim. Behav.* 123, 197–206. <https://doi.org/10.1016/j.anbehav.2016.10.036>
- Palmer, J.D., 1973. Tidal rhythms: the clock control of the rhythmic physiology of marine organisms. *Biological Reviews* 48, 377–418. <https://doi.org/10.1111/j.1469-185x.1973.tb01008.x>
- Pamela Delarue, E.M., Kerr, S.E., Lee Rymer, T., 2015. Habitat complexity, environmental change and personality: A tropical perspective. *Behav. Processes* 120, 101–110. <https://doi.org/10.1016/j.beproc.2015.09.006>
- Polak, T., Korine, C., Yair, S., Holderied, M.W., 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. *Journal of Zoology*. <https://doi.org/10.1111/j.1469-7998.2011.00808.x>
- Porter, R.K., Brand, M.D., 1995. Cellular oxygen consumption depends on body mass. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 269, R226–R228. <https://doi.org/10.1152/ajpregu.1995.269.1.r226>
- Prugh, L.R., Golden, C.D., 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J. Anim. Ecol.* 83, 504–514. <https://doi.org/10.1111/1365-2656.12148>
- Pulgar, J., Zeballos, D., Vargas, J., Aldana, M., Manriquez, P.H., Manriquez, K., Quijón, P.A., Widdicombe, S., Anguita, C., Quintanilla, D., Duarte, C., 2019. Endogenous cycles, activity patterns and energy expenditure of an intertidal fish is modified by artificial light pollution at night (ALAN). *Environ. Pollut.* 244, 361–366. <https://doi.org/10.1016/j.envpol.2018.10.063>
- Raap, T., Casasole, G., Costantini, D., AbdElgawad, H., Asard, H., Pinxten, R., Eens, M., 2016a. Artificial light at night affects body mass but not oxidative status in free-living nestling songbirds: an experimental study. *Sci. Rep.* 6, 35626. <https://doi.org/10.1038/srep35626>
- Raap, T., Pinxten, R., Eens, M., 2018a. Artificial light at night causes an unexpected increase in oxalate in developing male songbirds. *Conservation Physiology*. <https://doi.org/10.1093/conphys/coy005>
- Raap, T., Pinxten, R., Eens, M., 2016b. Artificial light at night disrupts sleep in female great tits (*Parus major*) during the nestling period, and is followed by a sleep rebound. *Environ. Pollut.* 215, 125–134. <https://doi.org/10.1016/j.envpol.2016.04.100>
- Raap, T., Pinxten, R., Eens, M., 2015. Light pollution disrupts sleep in free-living animals. *Sci.*

- Rep. 5, 13557. <https://doi.org/10.1038/srep13557>
- Raap, T., Thys, B., Grunst, A.S., Grunst, M.L., Pinxten, R., Eens, M., 2018b. Personality and artificial light at night in a semi-urban songbird population: No evidence for personality-dependent sampling bias, avoidance or disruptive effects on sleep behaviour. *Environ. Pollut.* 243, 1317–1324. <https://doi.org/10.1016/j.envpol.2018.09.037>
- Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V., Montiglio, P.-O., 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 4051–4063.
- Reddon, A.R., 2012. Parental effects on animal personality. *Behavioral Ecology* 23, 242–245. <https://doi.org/10.1093/beheco/arr210>
- Ringelberg, J., 2007. The photobehaviour of *Daphnia* spp. as a model to explain diel vertical migration in zooplankton. *Biol. Rev. Camb. Philos. Soc.* 74, 397–423. <https://doi.org/10.1111/j.1469-185X.1999.tb00036.x>
- Royauté, R., Greenlee, K., Baldwin, M., Dochtermann, N.A., 2015. Behaviour, metabolism and size: phenotypic modularity or integration in *Acheta domesticus*? *Animal Behaviour* 110, 163–169. <https://doi.org/10.1016/j.anbehav.2015.09.027>
- Sanders, D., Kehoe, R., Cruse, D., van Veen, F.J.F., Gaston, K.J., 2018. Low Levels of Artificial Light at Night Strengthen Top-Down Control in Insect Food Web. *Curr. Biol.* 28, 2474–2478.e3. <https://doi.org/10.1016/j.cub.2018.05.078>
- Sanders, D., Kehoe, R., Tiley, K., Bennie, J., Cruse, D., Davies, T.W., Frank van Veen, F.J., Gaston, K.J., 2015. Artificial nighttime light changes aphid-parasitoid population dynamics. *Sci. Rep.* 5, 15232. <https://doi.org/10.1038/srep15232>
- Sinn, D.L., Moltschaniwskyj, N. a., 2005. Personality traits in dumpling squid (*Euprymna tasmanica*): context-specific traits and their correlation with biological characteristics. *J. Comp. Psychol.* 119, 99–110. <https://doi.org/10.1037/0735-7036.119.1.99>
- Smith, B.R., Blumstein, D.T., 2008. Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19, 448–455. <https://doi.org/10.1093/beheco/arm144>
- Sneddon, L.U., 2003. The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology* 62, 971–975. <https://doi.org/10.1046/j.1095-8649.2003.00084.x>
- Speakman, J.R., 2013. Measuring energy metabolism in the mouse - theoretical, practical, and analytical considerations. *Front. Physiol.* 4, 34. <https://doi.org/10.3389/fphys.2013.00034>
- Spicer, J.I., Baden, S.P., 2000. Natural variation in the concentrations of haemocyanin from three decapod crustaceans, *Nephrops norvegicus*, *Liocarcinus depurator* and *Hyas araneus*. *Mar. Biol.* 136, 55–61.
- Spoelstra, K., Verhagen, I., Meijer, D., Visser, M.E., 2018. Artificial light at night shifts daily activity patterns but not the internal clock in the great tit (*Parus major*). *Proc. Biol. Sci.* 285. <https://doi.org/10.1098/rspb.2017.2751>
- Stamps, J.A., 2007. Growth-mortality tradeoffs and ?personality traits? in animals. *Ecology Letters* 10, 355–363. <https://doi.org/10.1111/j.1461-0248.2007.01034.x>
- Stamps, J.A., Briffa, M., Biro, P.A., 2012. Unpredictable animals: Individual differences in intraindividual variability (IIV). *Anim. Behav.* 83, 1325–1334. <https://doi.org/10.1016/j.anbehav.2012.02.017>
- Touzot, M., Teulier, L., Lengagne, T., Secondi, J., Théry, M., Libourel, P.-A., Guillard, L., Mondy, N., 2019. Artificial light at night disturbs the activity and energy allocation of the common toad during the breeding period. *Conserv Physiol* 7, coz002. <https://doi.org/10.1093/conphys/coz002>

- Troscianko, T., Benton, C.P., Lovell, P.G., Tolhurst, D.J., Pizlo, Z., 2009. Camouflage and visual perception. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 449–461.
- Truscott, Z., Booth, D.T., Limpus, C.J., 2017. The effect of on-shore light pollution on sea-turtle hatchlings commencing their off-shore swim. *Wildlife Research*.
<https://doi.org/10.1071/wr16143>
- Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. *Biological Reviews*. <https://doi.org/10.1111/j.1469-185x.2010.00164.x>
- Welbers, A.A.M.H., Welbers, A.A.M., van Dis, N.E., Kolvoort, A.M., Ouyang, J., Visser, M.E., Spoelstra, K., Dominoni, D.M., 2017. Artificial Light at Night Reduces Daily Energy Expenditure in Breeding Great Tits (*Parus major*). *Frontiers in Ecology and Evolution*.
<https://doi.org/10.3389/fevo.2017.00055>
- Westneat, D.F., Schofield, M., Wright, J., 2013. Parental behavior exhibits among-individual variance, plasticity, and heterogeneous residual variance. *Behavioral Ecology* 24, 598–604. <https://doi.org/10.1093/beheco/ars207>
- Westneat, D.F., Wright, J., Dingemanse, N.J., 2015. The biology hidden inside residual within-individual phenotypic variation. *Biol. Rev. Camb. Philos. Soc.* 90, 729–743.
- White, J.R., Meekan, M.G., McCormick, M.I., Ferrari, M.C.O., 2013. A Comparison of Measures of Boldness and Their Relationships to Survival in Young Fish. *PLoS ONE* 8, e68900. <https://doi.org/10.1371/journal.pone.0068900>
- White, S.J., Briffa, M., 2017. How do anthropogenic contaminants (ACs) affect behaviour? Multi-level analysis of the effects of copper on boldness in hermit crabs. *Oecologia* 183, 391–400. <https://doi.org/10.1007/s00442-016-3777-0>
- Widdows, J., Donkin, P., F. J Staff, Matthiessen, P., Law, R.J., Allen, Y.T., Thain, J.E., Allchin, C.R., Jones, B.R., 2002. Measurement of stress effects (scope for growth) and contaminant levels in mussels (*Mytilus edulis*) collected from the Irish Sea. *Marine Environmental Research* 53, 327–356. [https://doi.org/10.1016/s0141-1136\(01\)00120-9](https://doi.org/10.1016/s0141-1136(01)00120-9)
- Wyse, C.A., Selman, C., Page, M.M., Coogan, A.N., Hazlerigg, D.G., 2011. Circadian desynchrony and metabolic dysfunction; did light pollution make us fat? *Med. Hypotheses* 77, 1139–1144. <https://doi.org/10.1016/j.mehy.2011.09.023>
- Zubidat, A.E., Fares, B., Fares, F., Haim, A., 2018. Artificial Light at Night of Different Spectral Compositions Differentially Affects Tumor Growth in Mice: Interaction With Melatonin and Epigenetic Pathways. *Cancer Control* 25, 1073274818812908.
<https://doi.org/10.1177/1073274818812908>