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1 **The impact of streetlights on an aquatic invasive species: artificial light at night alters**
2 **signal crayfish behaviour.**

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4 John Rhidian Thomas^{1,2*}, Joanna James¹, Rhian Claire Newman^{1,2}, William D Riley², Siân W
5 Griffiths¹, Jo Cable¹

6 *Corresponding author

7 Email address: thomasjr6@cardiff.ac.uk

8 Telephone Number: +44 (0)29 20875729

9

10 ¹ School of Biosciences, Cardiff University, Cardiff, CF10 3AX, UK

11 ²The Centre for Environment, Fisheries & Aquaculture Science, Lowestoft Laboratory,
12 Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

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26 **Abstract**

27 Artificial light at night (ALAN) can significantly alter the behaviour, communication and
28 orientation of animals, and will potentially interact with other stressors to affect biodiversity.
29 Invasive, non-native species are one of the largest threats to freshwater biodiversity; however,
30 the impact of ALAN on such species is unknown. This study assessed the effects of ALAN at
31 ecologically relevant levels on the behaviour of a globally widespread invasive species, the
32 signal crayfish (*Pacifastacus leniusculus*). In experimental aquaria, crayfish were exposed to
33 periods of daylight, control (<0.1 lux) and street-lit nights to test two hypotheses: (1) signal
34 crayfish under natural conditions are nocturnal animals, spending more time in shelter during
35 the day, whilst active and interacting during the night, and (2) ALAN reduces crayfish activity
36 and intraspecific interactions, whilst increasing their propensity to use shelter. Our results
37 confirm that signal crayfish are largely nocturnal, showing peak activity and interaction levels
38 during control nights, whilst taking refuge during daylight hours. When exposed to short-term
39 simulated light pollution from a streetlight at night however, activity and interactions with
40 conspecifics were significantly reduced compared to control nights, whilst time spent in
41 shelters increased. By altering crayfish behaviour, ALAN may change the ecosystem impacts
42 of invasive crayfish in the wild. This study is the first to show an impact of ALAN on the
43 behaviour of an invasive, non-native species, and provides information for the management of
44 invasive crayfish in areas where ALAN is prevalent.

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46 **Keywords:** ecological light pollution; streetlight; crayfish behaviour; INNS; *Pacifastacus*
47 *leniusculus*; wildlife management

1. Introduction

Habitat degradation and invasive, non-native species can interact to significantly alter freshwater biodiversity (Dudgeon et al. 2006). An understudied form of habitat degradation is ecological light pollution caused by artificial light at night (ALAN) (Longcore & Rich 2004; Gaston et al. 2014), which can significantly affect biodiversity by altering species interactions, orientation and activity, and causing behavioural and physiological changes (Navara & Nelson 2007; Longcore & Rich 2004). In aquatic ecosystems, the behaviour of invasive, non-native species can lead to significant economic and environmental damage (Mack et al. 2000) and the unknown effects of ALAN on invasive, non-native species could potentially both exacerbate or ameliorate their destructive impacts through altering their behaviour.

A large proportion of ALAN is caused by street lighting (Longcore and Rich 2004) and there is a predicted 6% global increase per annum of streetlights (Hölker et al. 2010a). Within the UK, there are currently about 7.4 million streetlights in operation (Royal Commission on Environmental Pollution 2009). In the absence of ALAN, nocturnal light intensity varies with the phase of the moon, but is typically below 0.1 lux (Perkin et al. 2011, Gaston et al. 2014). Nocturnal lighting conditions have been consistent over long geological time scales, and only as a result of recent anthropogenic activity has there been a drastic change in night light conditions (Gaston et al. 2014). Small variations in light intensity can alter the behaviour of aquatic animals, with some species sensitive to light intensities as low as 10^{-7} lux (Moore et al. 2006). The spectral composition of street lights can also influence which animals may be affected (Davies et al. 2013), with broad spectrum light sources becoming more common in the UK as older, narrow spectrum bulbs are replaced (Royal Commission on Environmental Pollution 2009). Street lighting intensity recommendations in the UK currently indicate an average of 15 lux and minimum of 5 lux, whilst in North

America an average intensity of 20 lux is used (Riley et al. 2013). These nocturnal light intensities are likely to be having profound, and as yet largely unidentified, effects on a wide range of species.

More than 30% of vertebrates and 60% of invertebrates are nocturnal, and these organisms are likely to be affected by altered light regimes (Hölker et al. 2010b) since ALAN may lead to a ‘perpetual full moon’ effect (Longcore & Rich 2004). Nocturnal animals may become less active in the presence of artificial lighting; for example, male green frogs (*Rana clamitans*) call less during the breeding season (Bakker & Richardson 2006) and bat activity along commuting routes is drastically reduced (Stone et al. 2009). Conversely, diurnal animals may extend their activity into the night, for example, songbirds sing earlier in the morning and throughout the night, resulting in physiological fitness costs (Miller 2006; Dominoni et al. 2013, 2014). Predators may gain an advantage over prey as a result of ALAN, effectively exploiting a ‘night light niche’ (Longcore & Rich 2004). Whether it is edificationian reptiles, such as geckos (Perry & Fisher 2006), ground dwelling invertebrate communities (Davies et al. 2012) or various fish species (Becker et al. 2013), predators may increase their visual foraging success on prey attracted to the light source.

Compared to terrestrial ecosystems, there is a significant lack of research on the effects of ALAN in aquatic ecosystems (Longcore & Rich 2004; Perkin et al. 2011; Gaston et al. 2014). Additionally, to our knowledge, no study to date has examined the effects of ALAN on invasive, non-native species. Existing studies of aquatic species, however, provide evidence that ALAN can induce behavioural changes. For example, streetlights disrupt Atlantic salmon (*Salmo salar*) fry dispersal from hatching sites (Riley et al. 2013, 2015) as well as the onset of smolt seaward migration (Riley et al. 2012). Riparian street lighting can also influence freshwater ecosystems by disrupting invertebrate exchange between the river and riparian edge (Meyer & Sullivan 2013), reducing nocturnal drift rates (Holt & Waters

1967; Perkin et al. 2014; Henn et al. 2014) and interfering with flying adult dispersal (Perkin et al. 2011, 2013). Given the known effects of ALAN on freshwater organisms, it is likely that aquatic, non-native species will respond to ALAN, though this has never been assessed.

Among the most prolific, ecologically and economically costly aquatic invaders are freshwater crayfish (Holdich et al. 2009; Strayer 2010). Crayfish are keystone species (Geiger et al. 2005) and ecosystem engineers (Johnson et al. 2011; Stutzner et al. 2000) that can alter the structure and function of aquatic ecosystems by interacting with organisms on multiple trophic levels and changing habitat topography (James et al. 2014). In addition, the impacts of crayfish on aquatic ecosystems are predicted to be greater for invasive, non-native than for native species (James et al. 2014). Crayfish are largely regarded as nocturnal animals, though they may also show a degree of activity during the day (e.g. Edmonds et al. 2011; Miranda-Anyà 2004; Miguel & Aréchiga 1994). They are likely to be affected by ALAN, particularly as the light detection sensitivity of crayfish peaks at 570 nm (Kennedy & Bruno 1961), which is within the spectra of light emitted from commonly used high-pressure sodium streetlights (Royal Commission on Environmental Pollution 2009). The impact of ALAN from streetlights on both native and invasive crayfish however is unknown.

Here, we investigated the effects of ALAN on the behaviour of signal crayfish (*Pacifastacus leniusculus*). By exposing crayfish to daylight, control (<0.1 lux) and artificially lit nights, this study tested the following hypotheses: (1) signal crayfish are nocturnal, spending more time in shelter during daylight, whilst active and engaged in intraspecific interactions during the night, and (2) ALAN reduces signal crayfish activity and intraspecific interactions but increases their propensity to shelter.

2. Materials and methods

2.1 Animal origin and maintenance

Signal crayfish (*Pacifastacus leniusculus*) were caught using baited cylindrical crayfish traps ('Trappy Traps', Collins Nets Ltd., Dorset, UK) over a period of two weeks during spring 2014 from Dderw Farm pond, Llyswen, Brecon, South Wales (52°01'47.3"N 3°15'24.1"W) where ALAN is not present (<0.1 lux at the water surface at night). Traps were checked on a daily basis under trapping license number: CE068-N-315. Crayfish were transported to the Cardiff University aquarium facility and maintained in 100 L holding tanks (approx. 30 crayfish per tank) filled with dechlorinated water. Photoperiod was set at a 16 h light/ 8 h dark cycle. A desk lamp enclosed by neutral density filters (LEE Filters, Hampshire, UK) provided continuous, low night-time illumination at <0.1 lux (equivalent to a clear night at the trapping site) when the main aquarium lights were switched off. Daytime lighting at a similar intensity to that experienced at the trapping site on an overcast day was provided using full spectrum daylight mimicking bulbs (Sylvania T5 F13W/54-765 G5 Luxline Standard Daylight bulb) giving an intensity of 1000±50lux at the water surface. Crayfish in holding tanks were provided with a 2 cm pea gravel substrate, plant pot refugia and were fed daily with Tetra Crusta crayfish food pellets. Weekly 50% water changes were performed to maintain water quality. Animals were maintained under these conditions for at least two weeks to acclimatise to the laboratory conditions before the experiment began and any crayfish that showed signs of moulting, disease or lost appendages were excluded from the study. Blackout material was used to separate stock crayfish tanks from experimental aquaria. All applicable institutional and national guidelines for the care and use of animals were followed.

2.2 Influence of ALAN on crayfish behaviour

The effect of ALAN on signal crayfish behaviour was tested using a high-pressure sodium streetlight bulb (Phillips SON-T Pro 70w) in a luminaire with neutral density filter sheets (LEE Filters, Hampshire, UK), which provided a light intensity of 12±5 lux at the

water surface (similar to levels experienced in urban areas with street lighting; Riley et al. 2013). Infrared LED security cameras (3.6 mm SONY Hi-Res Super HAD, Waterproof IP68, Model: VN37CSHR-W36IR-25; RF-Concepts, Dundonald, UK) were installed above each experimental aquarium (tank measurements: L60 cm x W30 cm x D30 cm). Crayfish behaviour was recorded using a digital video recorder (embedded DVR-Video/LAN/USB. Model: LS8004MA- KGB Cameras; Innovative Technology, Wellingborough, UK). Each aquarium contained a pair of male signal crayfish and included a 2 cm pea gravel substrate as well as two plant pot refuges. Crayfish pairs were size matched to within 10% carapace length following Martin and Moore (2008) and one crayfish per pair was marked using yellow nail polish for individual identification.

Four pairs of crayfish were observed simultaneously (i.e. in four separate aquaria) and the experiment consisted of six trials (n = 24 pairs). During each trial, 32h of video was recorded per pair of crayfish. The timing of trials were as follows: on day one, crayfish were introduced to experimental aquaria on the opposite side to the shelters at 15:00hrs, allowing the animals time to acclimatise to the tanks before video recording began at 18:00hrs. Crayfish were recorded during daylight (1000 ± 50 lux) from 18:00hrs – 22:00hrs (daylight PM), followed by a night-time period 22:00hrs – 06:00hrs and then another daylight period from 06:00hrs – 10:00hrs (daylight AM) on day two (1000 ± 50 lux). The crayfish then remained in their tanks until the recordings were repeated at the same time on day two. In half of the trials, crayfish were exposed to control lighting (<0.1 lux) on night one and artificial lighting (12 ± 5 lux) on night two. In the other half of trials, the experiment was performed in reverse to determine whether the order of lighting regimes as well as the time spent in the experimental arena influenced the outcome of the study. There was no phased lighting transition between the day and night. The crayfish experienced exactly the same conditions in daylight PM and AM.

During video analysis, the time spent in shelter, at rest out of shelter and active out of shelter were recorded for each crayfish. A crayfish was defined as 'at rest' if it did not move for at least 3 min. Additionally, for each crayfish pair, the time spent engaged in agonistic interactions was recorded per hour. An aggressive interaction began when a crayfish approached its partner and physically engaged with it then ended when one of the pair retreated. Contact between individuals that did not result in aggression (e.g. climbing over each other) was not included in the analyses.

2.3 Statistical Analysis

A mean value for the number of seconds per hour ($s\ h^{-1}$) that each crayfish spent performing a particular behaviour (active, in shelter, interacting or stationary out of shelter) was calculated for the 8h night-time periods (control or artificially lit) and for the 4 h daylight AM or PM periods distinctly (a Wilcoxon Signed Rank test showed that activity was significantly different between daylight AM and PM [$V=766$, $P=0.014$] and therefore daylight AM and PM data were not pooled, despite lighting conditions being the same).

Two distinct analyses were performed: Analysis 1 on data from control days only (i.e. no artificial lighting), to determine whether the duration of crayfish behaviours differed between night and daylight (PM and AM), and Analysis 2 on night-time data only (control versus lit), to determine the effect of street lighting on crayfish behaviour. Separate GLMMs (Generalised Linear Mixed Models) for each type of behaviour included either 1) 'Time of Day' (i.e. night, daylight AM or PM) or 2) 'Lighting Condition' (control or lit) for the respective analyses. All models included 'Mark' to determine whether marking the crayfish influenced the outcome of the experiment. The carapace length of the individual crayfish (mm) was included in the models to determine whether crayfish size influenced behavioural parameters. 'Treatment' was included in all models to determine whether the order in which

the experiment was conducted (i.e. order of control and lit nights) influenced crayfish behaviour. In all models, individual crayfish were assigned a code, and this 'Crayfish ID' was nested within 'Tank Number' that was nested within 'Trial' and included as a random term, to account for pseudoreplication, since each crayfish was recorded twice, and also to account for variation between the four tanks and between trials. This nested random term was kept within all final models.

All models were refined by stepwise deletion, manually removing the least significant term and re-running the model until only significant ($P < 0.05$) terms remained (Crawley 2007). Model fit was assessed using residual plots as recommended by Pinheiro and Bates (2000). All statistical analyses were performed using R statistical software, version 3.1.2 (R Core Team 2014). All GLMMs were performed using the 'nlme' package unless otherwise stated (Pinheiro et al. 2014). Planned contrasts between groups were examined by post-hoc TukeyHSD tests using the 'lsmeans' package (Lenth and Hervé 2015).

3. Results

Signal crayfish spent significantly more time active during control (<0.1 lux) nights when compared to daylight PM ($t_{94} = -12.87$, $P < 0.001$) and daylight AM ($t_{94} = -11.60$, $P < 0.001$; Fig. 1, Table 1). Activity during all three periods was influenced by the carapace length of the individual, i.e. larger individuals were more active ($t_{23} = 2.184$, $P = 0.039$). Exposure to ALAN significantly reduced signal crayfish activity ($t_5 = 6.742$, $P < 0.001$, Fig. 1, Table 2) compared to control (<0.1 lux) nights. Across all lighting conditions however, crayfish activity was positively correlated with carapace length ($t_{23} = 3.475$, $P = 0.002$).

Signal crayfish spent significantly less time sheltering during control (<0.1 lux) nights compared to daylight (daylight PM, $t_{94} = 8.560$, $P < 0.001$ and daylight AM $t_{94} = -7.751$, $P < 0.001$; Fig. 1, Table 1). Exposure to ALAN led to individuals spending significantly more

time in shelter ($t_{47} = -4.389$, $P < 0.001$, Fig. 1, Table 2) compared to control nights, though larger individuals were less likely to shelter than smaller ones ($t_{23} = -2.869$, $P = 0.009$).

Pairs of signal crayfish interacted for significantly more time during control (<0.1 lux) nights when compared to daylight (daylight PM $t_{94} = -11.06$, $P < 0.001$ and daylight AM $t_{94} = -7.75$, $P < 0.001$; Fig. 1, Table 1). When exposed to ALAN, crayfish pairs interacted for significantly less time ($t_{47} = 4.386$, $P < 0.001$, Fig. 1) compared to control (<0.1 lux) nights.

Signal crayfish spent more time at rest and out of shelter during control nights (<0.1 lux) compared to daylight PM ($t_{94} = -3.637$, $P = 0.001$) and daylight AM ($t_{94} = 9.149$, $P < 0.001$), however ALAN did not have a significant effect (Table 2). Both 'Treatment' (the order of control and lit nights) and 'Mark' had no significant effect on any of the behavioural parameters measured (Tables 1 and 2).

4. Discussion

The current study provides the first evidence that artificial light at night (ALAN) at levels typically encountered in urban areas significantly affects the behaviour and activity of an invasive, non-native species. Compared to control nights, signal crayfish (*Pacifastacus leniusculus*) individuals spent less time active and engaged in fewer intraspecific interactions when exposed to ALAN, whilst their propensity to shelter increased. Further, our study confirms that signal crayfish largely exhibit nocturnal activity under natural lighting regimes (Edmonds et al. 2011; Miranda-Anyà 2004; Miguel & Aréchiga 1994). Since crayfish are keystone species (Geiger et al. 2005) and ecosystem engineers (Johnson et al. 2011; Stutzner et al. 2000), altered activity patterns as a result of artificial lighting may change their effects on ecological communities. Crayfish, especially invasive species such as signal crayfish, influence many organisms directly through predation (James et al. 2014) and reduced activity may lead to reduced foraging efficiency.

Crayfish alter multiple characteristics of riverbeds (Statzner et al. 2000; Statzner & Peltret 2006) often increasing bioturbation and sediment movement through high levels of activity (Creed & Reed 2004; Dorn & Wojdak 2004). Higher suspended sediment load in rivers directly impacts organisms with sensitive gills, such as the native white-clawed crayfish (*Austropotamobius pallipes*; see Rosewarne et al. 2014) as well as reducing the flow of oxygen through gravel to salmonid eggs and embryos (Greig et al. 2005). By suppressing nocturnal crayfish activity, ALAN could reduce the rate of sediment mobilisation by crayfish in rivers. Conversely, by increasing their need for shelter, ALAN could also increase signal crayfish burrowing behaviour (Guan 1994), which would increase suspended sediment levels and cause riverbank collapse.

In the current study, signal crayfish spent more time in shelter under street-lit conditions compared to control nights. Shelter is an important resource for which crayfish compete (Bergman & Moore 2003) since they are highly vulnerable to predation by large fish species such as perch, carp, and eels (Blake & Hart 1995; Hill & Lodge 1999). Additionally, in some areas, riverine mammals such as otters may feed mainly on crayfish (Ilhéu et al. 2003). Increased shelter use by signal crayfish at night may increase competition with native crayfish, especially if native species of crayfish are similarly affected by artificial night lighting. This could lead to exacerbated competitive exclusion of native crayfish species, leading to population decline as a result of increased predation susceptibility of the native crayfish (Dunn et al. 2009). Increased competition for shelter could also result in competitive exclusion and subsequent predation of subordinate crayfish, which are usually young or female individuals (Ilhéu et al. 2003), leading to changes in population structure. Native fish such as bullheads (*Cottus gobio*) and salmon (*Salmo salar*) also rely on shelter for protection from predators (Bubb et al. 2009; Griffiths et al. 2004). Bullheads are mostly nocturnal, but

spend around 60% of the night in shelter (Bubb et al. 2009) and nocturnal competitive exclusion by signal crayfish could increase in areas of sympatry affected by ALAN.

The current study shows that ALAN significantly reduces the duration of intraspecific interactions between signal crayfish. Such interactions among crayfish are key in establishing dominance hierarchies (Issa et al. 1999) and may typically occur at certain time periods. For example, intraspecific interactions among groups of marbled crayfish (*Procambarus fallax f. virginalis*) in the laboratory coincide with transitions between light and dark and vice-versa (Luna et al. 2009). Disrupted agonistic interactions between signal crayfish in areas of ALAN could interfere with establishment of dominance hierarchies leading to changes in population dynamics.

The success of invading species can depend on interactions with existing fauna, but also local environmental factors (Blackburn et al. 2014). ALAN in areas where non-native species are introduced may initially hamper the establishment and subsequent spread of these species. For signal crayfish in the UK, which we confirm are largely nocturnal, dispersal is around $1.8 \text{ km}^{-1}\text{yr}$ in the River Lee, London (James et al. *unpublished*), and their daily movement is over double that of the native white-clawed crayfish, *Austropotamobius pallipes* (see Bubb et al. 2006). Street lighting may slow dispersal rates of invasive species if activity levels and movement are reduced at night, especially for new, nocturnally dispersing invaders, which may not have experienced ALAN in their native range. It is possible, however, that although signal crayfish and other invasive, non-native species may be initially discouraged from dispersing to new areas in the presence of ALAN, they may become acclimatised to the unnatural lighting conditions. Additionally, streetlights with different spectral compositions may affect species differentially (Davies et al. 2013), and it is difficult to predict how this will influence interspecific interactions, and subsequent invasion success of different species.

In conclusion, the current study has demonstrated that, at least in the short term, ALAN significantly reduces the activity and duration of interactions among invasive, non-native signal crayfish, and increases their nocturnal shelter use. The implications of the current study suggest that reduced crayfish activity may on the one hand be beneficial to invaded ecosystems through potentially decreasing the amount of predation and suspended sediment caused by crayfish. Conversely, an increased propensity of crayfish to shelter may increase competition with native species as well as causing an increase in burrowing behaviour, causing riverbank collapse and increased siltation (Guan 1994). Future studies should assess the long-term effects of ALAN in the field, especially on threatened European species, such as the white-clawed crayfish. In Britain, the future of this species largely depends on managing ‘Ark sites’, which are secure water bodies that can support and protect white-clawed crayfish populations from disturbances such as pollution and non-native crayfish (Rees et al. 2011). If the persistence of this species is partially reliant on the establishment of ‘Ark sites’ (Rees et al. 2011; Holdich et al. 2009), selection of these sites should consider the effect of ALAN. From a management perspective, this study adds to the growing body of evidence that ALAN, as a result of broad-spectrum street lighting, affects the behaviour of aquatic animals and has the potential to disrupt ecological systems.

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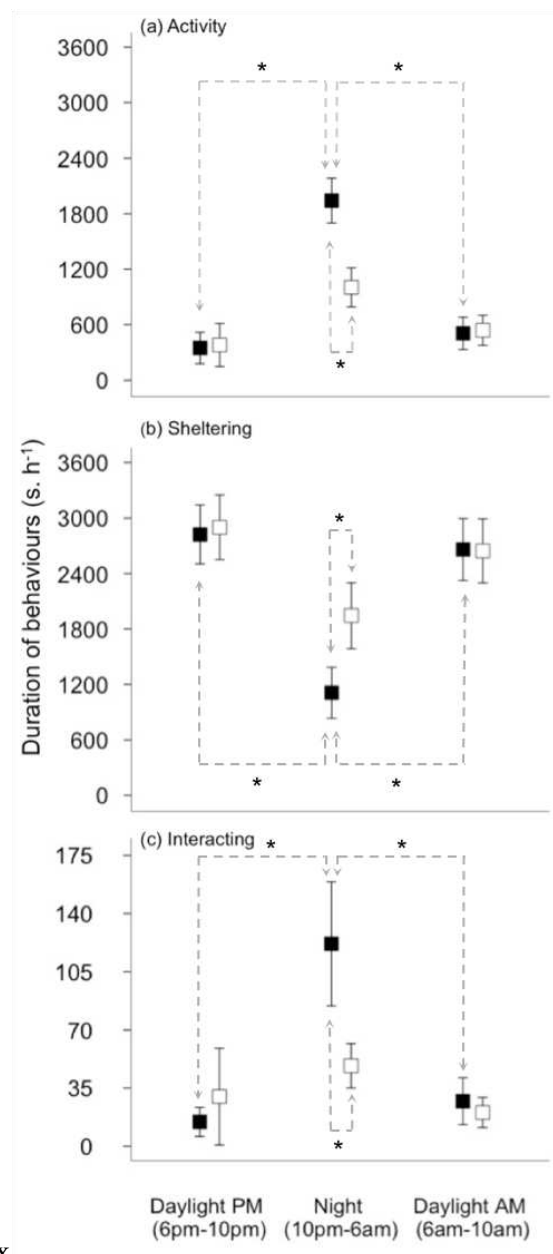
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Fig. 1 *Pacifastacus leniusculus* activity. Duration (s h⁻¹) individuals spent during three time periods: daylight PM, night and daylight AM (a) active (n=48), (b) sheltering (n=48) and (c) interacting in pairs (n=24). Light intensity during daylight PM (6pm-10pm) and daylight AM (6am-10am) was 1000±50 lux. Mean values (bars show 95% CI) are presented separately for crayfish exposed to control lighting conditions at night (filled squares; <0.1 lux) and crayfish exposed to artificial light at night (unfilled squares; 12±5 lux). Pairwise comparisons are shown using dashed lines, and significant differences are denoted by an asterisk.

Table 1 - Results from stepwise refinement of Generalised Linear Mixed models and post-hoc pairwise comparisons using TukeyHSD tests performed during Analysis 1 on control night data, examining differences in signal crayfish behavior between control night (<0.1lux) and

daylight hours. R^2 values obtained by recreating final models in the lme4 package (Bates et al. 2014). Abbreviations are as follows: TOD = time of day, CL = carapace length, Treat = treatment group, df = degrees of freedom, S.E. = standard error, t = t test statistic value. Significant results (at $P < 0.05$ are highlighted in bold).

Dependent variable	R^2		Fixed terms	LRT Chi ²	df	p-value	Pairwise comparisons	Estimate	S.E.	df	t-value	p-value	
	Fixed	Random											
<i>Activity</i>	0.533	0.106	TOD	114.9	2	<0.001	DayPM-Night	-1593.6	123.8	94	-12.87	<0.001	
								DayPM-DayAM	-157.9	123.8	94	-1.275	0.412
								Night-DayAM	1435.7	123.8	94	11.60	<0.001
					CL	4.526	1	0.033					
		Treat	1.411	1	0.235								
		Mark	1.567	1	0.211								
<i>Sheltering</i>	0.333	0.134	TOD	64.3	2	<0.001	DayPM-Night	1713.6	200.2	94	8.560	<0.001	
								DayPM-DayAM	161.8	200.2	94	0.808	0.699
								Night-DayAM	-1551.8	200.2	94	-7.751	<0.001
					CL	3.182	1	0.074					
		Treat	1.283	1	0.257								
		Mark	0.696	1	0.404								
<i>Interacting*</i>	0.405	0.181	TOD	905.6	2	<0.001	DayPM-Night	-8.032	0.726	94	-11.06	<0.001	
								DayPM-DayAM	-1.389	0.726	94	-1.911	0.141
								Night-DayAM	6.644	0.726	94	9.149	<0.001
					CL	1.890	1	0.169					
		Treat	0.002	1	0.961								
		Mark	0.001	1	0.993								
<i>Stationary*</i>	0.100	0.214	TOD	18.80	2	<0.001	DayPM-Night	-29.13	8.01	94	-3.637	0.001	
								DayPM-DayAM	3.878	8.01	94	0.484	0.879
								Night-DayAM	33.00	8.01	94	4.121	<0.001
					CL	2.352	1	0.125					
		Treat	1.633	1	0.201								
		Mark	1.153	1	0.283								

* square root transformed

** log transformed

Table 2 - Results from stepwise refinement of Generalised Linear Mixed models and post-hoc pairwise comparisons using TukeyHSD tests performed during Analysis 2 on lit versus unlit data, examining differences in signal crayfish behavior between control nights (<0.1lux) and artificially lit nights (12±5 lux). R^2 values obtained by recreating final models in the 'lme4' package (Bates et al. 2014). Abbreviations are as follows: Light = night lighting conditions, CL = carapace length, Treat = treatment group, df = degrees of freedom, S.E. = standard error, t = test statistic value. Significant results (at $P < 0.05$ are highlighted in bold).

Dependent variable	R^2		Fixed terms	LRT Chi ²	df	p-value	Pairwise comparisons	Estimate	S.E.	df	t-value	p-value
	Fixed	Random										
<i>Activity</i>	0.339	0.135	Light	36.93	1	<0.001	Unlit - Lit	937.99	139.13	47	6.742	<0.001
			CL	10.87	1	<0.001						
			Treat	1.57	1	0.210						
			Mark	1.69	1	0.193						
<i>Sheltering</i>	0.201	0.226	Light	16.64	1	<0.001	Unlit - Lit	-833.73	189.94	47	-4.389	<0.001
			CL	7.78	1	0.005						
			Treat	0.256	1	0.613						
			Mark	1.187	1	0.276						
<i>Interacting*</i>	0.134	0.211	Light	17.76	1	<0.001	Unlit - Lit	1.076	0.245	47	4.386	<0.001
			CL	3.34	1	0.675						
			Treat	0.015	1	0.902						
			Mark	0.001	1	0.994						
<i>Stationary**</i>	0.017	0.244	Light	0.341	1	0.560	Unlit - Lit	-	-	-	-	-
			CL	0.297	1	0.586						
			Treat	0.246	1	0.620						
			Mark	0.410	1	0.522						

*log(x)+1 transformed

**square root transformed

