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Artificial skyglow disrupts celestial migration at night

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Understanding of the ecological impacts of direct outdoor lighting has improved substantially over the last decade [1-3]. Those of artificial skyglow – artificial light that is scattered in the atmosphere and reflected back to the ground - have received comparatively little attention [4]. Artificial skyglow extends the influence of direct lighting out to hundreds of kilometres from direct sources (for example street lights). It is the most geographically widespread form of light pollution, affecting 23% of the world's land surface (between 75°N and 60°S) [5] at illuminances which are two orders of magnitude lower (0.2 and 0.5 lx) than light pollution from direct artificial light (typically 10 - 100 lx), and greater than moonlight (0.1 - 0.3 lx) and the Milky Way (0.001 lx). Numerous organisms across the animal kingdom that orientate during migrations using lunar compasses [6-9] are vulnerable to artificial skyglow across large (10-100km) spatial scales. We demonstrate that artificial skyglow disrupts nightly migrations undertaken by the amphipod *Talitrus saltator* that are guided by the sky position of the moon [9-10].

T. saltator lives in burrows in the upper shore of sandy beaches, migrating seawards nightly to forage among strand line algae, and returning to refuge on the upper shore to avoid dessication, predation and immersion. These migrations are essential for the fitness and survival of *T. saltator*, and as with many species which undergo light guided migrations, deleterious impacts on them may have clear ramifications for the viability of populations.

The impact of experimentally introduced artificial skyglow (0.2 lx diffused cool white LED light) on *T. saltator* migrations was quantified during a manipulative field experiment carried out over 19 nights on Cable Bay beach, UK (53°12'25.8"N, 4°29'53.9"W) from late June until early September 2019 spanning three monthly lunar cycles. Cable Bay is a sandy shore located 13km from its nearest urban centres Llangefni (population ~5,000) and Holyhead (population ~13,000) and experiencing 77.2 $\mu cd/m^2$ of artificial sky brightness [5] (typical natural sky brightness = 174 $\mu cd/m^2$; pristine sky brightness = 1.7 $\mu cd/m^2$ [5]). A cool white LED was selected to be representative of the increasingly predominant exterior light source contributing to city skyglow. We quantified the probability of *T. saltator* carrying out their nocturnal migrations and, for individuals that migrated, the directions in which these migrations occurred. All behavioural observations were conducted in situ at night in the presence and absence of the artificial skyglow treatment; during full moon, and new moon; and under clear (< 3 Okta) and cloudy (> 4 Okta) conditions. Migration behaviour was assessed for 960 individuals, 120 individuals in each treatment combination (Artificial skyglow treatment*Moon phase*Cloud cover). Experimental runs were constrained to control for variable climatic factors (for example, onset of rainfall) and when the sun was more than -12° below the horizon (nautical twilight).

Our results demonstrate that artificial light equivalent in illuminance to artificial skyglow impacts celestial guided nightly migrations undertaken by the sandhopper *T. saltator*. Firstly, artificial skyglow reduced the probability that *T. saltator* undertook these migrations during the full moon under clear sky conditions, and during the new moon irrespective of cloud cover (Figure 1A, Table S2). All predictor variables and their interactions (~Artificial skyglow treatment*Moon phase*Cloud cover) were included in the most parsimonious model describing variance in the probability that *T. saltator* underwent migration on introduction to an experimental arena (Table S1). Artificial skyglow was included in the top 14 out of 19 candidate models (Table S1). The selected model was 10.9 AIC points lower than the next ranking candidate model, had a high relative likelihood (0.993) compared to all remaining candidate models (ranging from 0-0.004, Table S1), and described significantly more variance in the probability that *T. saltator* underwent migration than a null intercept only model ($\chi^2 = 81.73$, $p<0.001$). The presence of artificial skyglow significantly reduced the probability that *T. saltator* underwent migrations during full moon under clear conditions (Estimate: 1.87±0.35 se; $Z = 5.29$; $p<0.0001$), and during new moon under both clear (Estimate: 0.92±0.30 se; $Z = 3.12$; $p<0.01$) and cloudy (Estimate: 1.03±0.3 se; $Z = 3.30$; $p<0.01$) conditions.

Secondly, even when migrations were undertaken during exposure to artificial skyglow, *T. saltator* did not move in the expected prevailing direction, or any prevailing direction under most conditions (Figure 1B, Table S2). *T. saltator* migrated in the expected shoreward direction (to forage) in the absence of artificial skyglow when the moon was full and the sky was clear (Figure 1B, Table S2), but did not move in a quantifiable direction in the presence of artificial skyglow during the same moon phase and cloud cover conditions (Figure 1B, Table S2). *T. saltator* migrated in the landward direction (towards refuge) in the presence of experimentally introduced artificial skyglow when the moon was new and the sky was clear (Figure 1B, Table S2), but no specific direction was quantifiable in the absence of artificial skyglow under the same moon phase and cloud conditions (Figure 1B, Table S2). In this latter scenario, individuals responded either to other environmental stimuli (for example a rising tide), or could be using the artificial skyglow treatment as the primary orientation cue in the absence of moonlight. *T. saltator* migration did not, however tend towards any quantifiable direction under cloudy conditions, irrespective of whether artificial skyglow was experimentally introduced (Figure 1B, Table S2).

These results indicate that artificial skyglow disrupts the nocturnal celestial migrations of *T. saltator* by reducing the probability of such behaviour, and disrupting the lunar compass used by this species to orientate during long distances. Skyglow is the most geographically widespread form of light pollution, which our results show has demonstrable impacts on biological processes that are guided by nighttime celestial light cues, and critical to organism fitness and survival across a broad range of taxa [6-9]. The potential for skyglow to impact the population dynamics and biogeographical distributions of taxa that undergo celestial migrations is clear. A renewed focus on the ecological impacts of artificial skyglow is urgently needed to fully understand the extent to which it is shaping the natural environment.

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Author Contributions

Conceptualization, T.D; Methodology, D.T. and T.D; Investigation; D.T, T.D. and S.T.; Formal Analysis, D.T. and T.D. Writing-Original Draft, D.T; Writing-Review and Editing, T.D., S.T., D.T. and S.J.; Resources, T.D. and S.J.; Funding Acquisition, T.D. and S.J.; Project Administration, T.D. and S.J.

Declaration of Interests

The authors declare no competing interests.

Figure Legends

Figure 1. The impact of artificial skyglow on nighttime celestial migrations undertaken by *T. saltator*. A: The probability that *T. saltator* undertake nightly migrations under artificial skyglow (grey bars) and natural light conditions (black bars) was compared during Full and New moon under clear and cloudy skies. Error bars correspond to standard errors. Asterisks represent significant differences between treatments (**$P \leq 0.01$, ***$P \leq 0.001$). B: For individuals that underwent migrations, the directions of these movements were quantified for each artificial skyglow treatment*moon phase*cloud cover combination (denoted by bar colours and symbols in A). Dashed red lines show the expected migration directions either the seaward

direction (SWW) towards forage or landwards (NEE) towards refuge. Dashed green lines show observed migrations directions that were statically significant at the 95% confidence level. Number of sandhoppers that followed each direction is illustrated by the numbers within each concentric circle.

Supplemental Information

Supplemental Experimental Procedures

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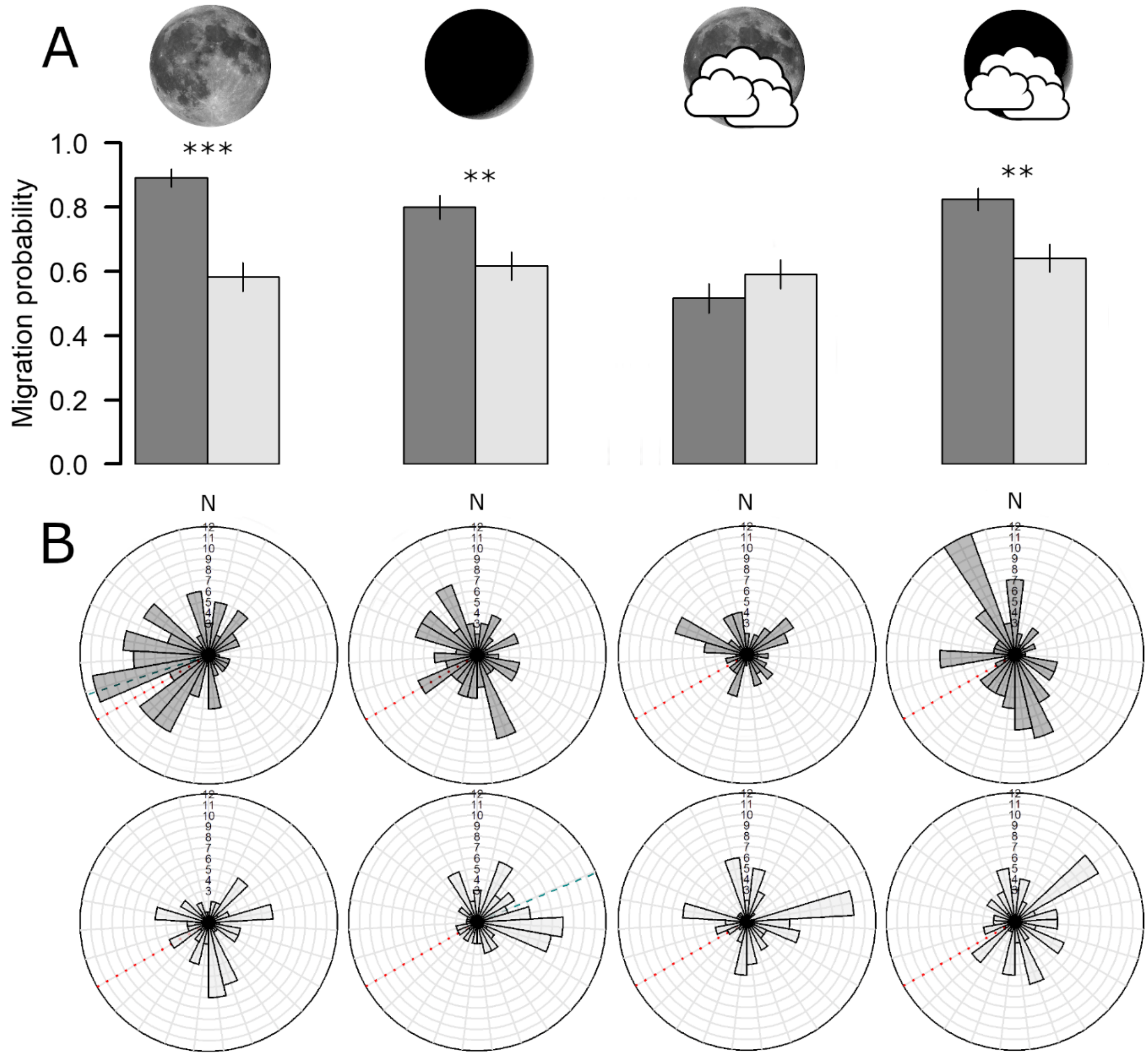

Figure 1. The impact of artificial skyglow on nighttime celestial migrations undertaken by *T. saltator*. A: The probability that *T. saltator* undertake nightly migrations under artificial skyglow (grey bars) and natural light conditions (black bars) was compared during Full and New moon under clear and cloudy skies. Error bars correspond to standard errors. Asterisks represent significant differences between treatments (**$P \leq 0.01$, ***$P \leq 0.001$). B: For individuals that underwent migrations, the directions of these movements were quantified for each artificial skyglow treatment*moon phase*cloud cover combination (denoted by bar colours and symbols in A). Dashed red lines show the expected migration directions either the seaward direction (SWW) towards forage or landwards (NEE) towards refuge. Dashed green lines show observed migrations directions that were statically significant at the 95% confidence level. Number of sandhoppers that followed each direction is illustrated by the numbers within each concentric circle.

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Model	D.f.	AICc	Weight
*~ ALAN*Moon phase * Cloud cover*	9	1133.6	0.993
*~ALAN*Cloudiness + Moon phase*Cloud cover*	7	1144.5	0.004
*~ALAN*Moon phase + ALAN*Cloud cover + Moon phase*Cloud cover*	8	1145.4	0.003
*~ALAN*Cloud cover + ALAN*Moon phase*	7	1155.2	0.000
*~ALAN + Moon phase*Cloud cover*	6	1155.4	0.000
*~ALAN*Cloud cover + Moon phase*	6	1155.6	0.000
*~ALAN*Moon phase + Moon phase*Cloud cover*	7	1155.7	0.000
*~ALAN*Cloud cover*	5	1160.3	0.000
*~ALAN*Moon phase + Cloud cover*	6	1167.1	0.000
~ALAN + Moon phase + Cloud cover	5	1167.2	0.000
~ALAN + Cloud cover	4	1171.6	0.000
~ALAN + Moon phase	4	1172.1	0.000
*~ALAN*Moon phase*	5	1172.1	0.000
~ALAN	3	1176.4	0.000
*~Moon phase * Cloud cover*	5	1181.3	0.000
~Moon phase + Cloud cover	4	1191.8	0.000
~Cloud cover	3	1196.3	0.000
~Moon phase	3	1196.8	0.000
Null	2	1201.1	0.000

Table S1. Selection of the most parsimonious model describing variance in the probability that *T. saltator* underwent migration (Figure 1, Table 1). A global model (~Artificial skyglow treatment*Moon phase*Cloud cover) and all nested candidate models, including a null, were compared using the value of Akaike's Information Criterion (AIC), and that with lowest value of AIC considered most parsimonious. The experimental run number within each unique treatment combination was included as a random effect [~(1|Experimetal Run)] to control for repeated measures of either 10 or 20 individuals within each assay.

Moon phase	Cloud cover	Light treatment	*n*	**Prevailing migration direction**[a]						**Mean direction of migration**[b]	
				Any		Seaward		Landward			
				Z	*p*	*Z*	*p*	*Z*	*p*	U^2	*p*
Full	Cloudy	Artificial	75	0.13	0.417	-	-	-	-	0.13	0.100
		Natural	65	0.09	0.606	-	-	-	-		
	Clear	Artificial	70	0.18	0.212	-	-	-	-	0.39	**< 0.01**
		Natural	105	0.32	**< 0.01**	0.18	**< 0.01**	-	-		
New	Cloudy	Artificial	74	0.13	0.248	-	-	-	-	0.21	**0.030**
		Natural	96	0.13	0.248	-	-	-	-		
	Clear	Artificial	77	0.30	**< 0.01**	-0.19	0.991	0.30	**< 0.01**	0.45	**< 0.01**
		Natural	101	0.14	0.248	-	-	-	-		

Table S2. The impact of experimentally introduced artificial skyglow on the direction of night-time intertidal migrations undertaken by *T. saltator* Results are reported for the impact of artificial skyglow during full moon and new moon, and under clear and cloudy sky conditions. *P* values adjusted for multiple tests using False Discovery Rate. [a] Established using Raleigh's test of uniformity, assessing the significance of the mean direction and whether it corresponds to the *expected direction.* [b] Established using Watson's test of homogeneity between two samples to see if artificial skyglow changed *the mean* migration *direction* (either significant or non-significant).

Supplemental Experimental Procedures

Experimental design and data collection

Individuals were collected by hand from across the study location and introduced into a 50 cm diameter transparent cylindrical arena in which 27 pit-fall traps (3.5 cm in diameter and 7 cm height) were placed around its inner circumference, one for each 13.3 degrees of compass direction. The arena was partially filled with sieved dry sand collected from the beach to provide a realistic substrate, levelled with a 0° inclination with respect to the ground and placed landwards from the strand line. Individuals were introduced to the middle of the arena using a 4 cm diameter, 20 cm long PVC tube. The tube was removed after ten seconds to allow individuals to acclimatise. In each experimental run, either 10 or 20 individuals were introduced to the arena every 30 seconds (run duration either 300s and 600s), a suitable length of time determined from pilot investigations for individuals to migrate to the edge of the arena and fall into pitfall traps. To simulate artificial skyglow with an even dispersion of light, we placed a battery powered cool white LED within a diffusing sphere (4 cm diameter) and suspended it 150 cm above the centre of the cylindrical arena achieving a ground level illuminance of 0.211 lx. It was assumed that an individual had migrated if it was found in a pit-fall trap, quantified after every 20 individuals introduced. The probability that *T. saltator* underwent migration towards the edge of the arena was scored for each individual as 1 (migrated) or 0 (did not migrate). For those individuals that carried out migratory behaviour, the direction of migration and its accuracy (whether it followed an expected direction) were quantified by counting the number of individuals collected in each of the pit-fall traps.

2.2. Statistical analysis

All statistical analyses were carried out in R version 3.5.1. The impact of artificial skyglow, moon phase and cloud cover on the probability that individuals migrated was analysed using a Generalised Linear Mixed Effects Model (GLMER; CRAN: lme4) with a binomial error distribution. The experimental run number within each unique treatment combination was included as a random effect [~(1|Experimetal Run)] to control for repeated measures of either 10 or 20 individuals within each assay. The most parsimonious combination of predictor variables nested within a global model, including all 2nd and 3rd order interactions (~Light treatment*Moon phase*Cloud cover), was identified as that with the lowest value of Akaike's Information Criterion (AIC) using [CRAN: MuMIn (Dredge)]. Model selection was further validated using AIC weights, and the significance of the selected model was tested against a null intercept only model. Between and within treatment group responses were quantified by calculating pairwise contrasts within the selected model (CRAN: emmeans).

For individuals that migrated, the changes in mean migration direction (° from North) were analysed using circular statistics in CRAN:circular. The package does not support the analysis of complex interactions, hence the impact of artificial skyglow on the response variables was quantified by comparison with the controls independently for each Moon phase:Cloud cover treatment combination, with *P*-values adjusted for the number of tests using False Discovery Rate. Rayleigh tests were used to determine whether there was a predominant/significant mean direction (a unimodal distribution of the data) which corresponded to the expected seaward direction (towards food source) (SW 240°). Watson tests were used to quantify whether the presence of artificial skyglow changed the mean migration direction.