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Does Artificial Light at Night Alter the Subsequent Diurnal Behavior of a Teleost Fish?

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Abstract Artificial light at night (ALAN) is one of the fastest growing anthropogenic disturbances to animals across many ecosystems, yet little is known about how ALAN influences fish and aquatic ecosystems. Our current understanding of the effects of ALAN on fish behavior and physiology tend to be based on research conducted during night, with comparatively little research on whether ALAN influences subsequent behavior during diurnal periods. We used wild-caught Bluegill *Lepomis macrochirus* as a model to assess whether ALAN of differing intensities comparable to what would be experienced in the wild near human-altered landscapes (i.e., 0.5 lux, 4 lux, 9 lux) alters subsequent diurnal behavior relative to controls (i.e., dark, 0 lux). We assessed a number of behavioral traits in a laboratory setting known to relate to performance and fitness in wild teleost fish including exploration, activity levels, space usage, and risk aversion. Exploration behavior, space use, and risk-taking behaviors were similar among treatments. Only locomotor activity differed among treatments with Bluegill in the 0.5 and 9 lux treatments swimming significantly less than controls after being exposed to ALAN overnight. This difference in behavior was found at light intensities commonly found at waterways today and thus may already be affecting fish communities and aquatic ecosystems.

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1 Introduction

Artificial light at night (ALAN) is a form of pollution where an area is exposed to light from a non-natural source that is brighter than the natural light levels at night (Cinzano et al. 2001; Falchi et al. 2016). ALAN can come from two sources; either a direct source, such as streetlights or dock lights (Gaston et al. 2015) or from artificial light reflected off the clouds and atmosphere known as skyglow (Kyba et al. 2011). Direct light is brighter than skyglow, but skyglow can reach much farther distances and can therefore disturb animals and ecosystems far from urban areas (Kurvers et al. 2018). ALAN has become a very common form of anthropogenic pollution, with much of the world being affected by skyglow, which is brighter than the natural light the moon and stars would provide (Davies et al. 2013; Gaston et al. 2015). ALAN is also expanding with an estimated increase of 6 percent per year (Hölker et al. 2010; Pulgar et al. 2019). Importantly, ALAN is most rapidly expanding along coastlines in both marine and freshwater systems (Gaston et al. 2015; Reid et al. 2019). Therefore, aquatic ecosystems will be exposed to brighter and larger expanses of ALAN in the coming years. Despite this expected increase in light pollution in aquatic environments, there has been limited research on how ALAN affects fish, compared to many other taxa.

Many animals have evolved daily and seasonal processes based around constant day-night cycles including aspects of reproduction that are being disrupted by ALAN (Longcore and Rich 2004; Sanders et al. 2020; Secondi et al. 2020). For example, many species of fish, such as the European Roach (*Rutilus rutilus*), require a certain level of darkness for reproduction and regulation of the endocrine system (Brüning et al. 2018). Exposure to ALAN of 15 lux (comparable to nocturnal street lighting) suppressed the reproductive hormones in European Roach, which could delay or stop their reproductive cycle (Brüning et al. 2018). ALAN can also impair fish reproduction in other ways. For example, Foster et al. (2016) reported that ALAN from shoreline light (both consistent low-level light and short duration high intensity light) increased the locomotor activity of nest guarding male Smallmouth Bass (*Micropterus dolomieu*) relative to controls. Moreover, research suggests that fish eggs in bright areas hatch earlier compared to eggs laid in darker areas (Brüning et al. 2011) or may not hatch at all (Fobert et al. 2019). Finally, many fish migrate at night to reach spawning grounds and the brightness of ALAN can prevent normal nocturnal migration (Jonsson 1991). Clearly, ALAN has the potential to influence the timing and reproductive biology of fish.

ALAN can also have dramatic effects on fish outside of the reproductive period. For example, ALAN is known to attract some fish species, particularly larger predators to brightly lit areas (Becker et al. 2013), where direct ALAN is sufficiently bright to allow diurnal predators to forage at night (Diehl 1988; Czarnecka et al. 2019). Some prey fish have also been shown to use visual based anti-predator behavior, such as schooling, that would be impossible to coordinate at natural nighttime light levels, potentially reducing their risk of predation (Becker et al. 2013). Fish that have been exposed to ALAN have also shown tendencies to swim farther away from the walls and spend more time in the open areas of their behavioral tanks, which could expose them to higher levels of predation (Kurvers et al. 2018). Pulgar et al. (2019) found that ALAN can also affect the activity level of fish, showing that the intertidal rockfish (*Girella laevifrons*) swam more and had higher metabolic rate after being exposed to ALAN. However, almost all of the aforementioned studies took place during nighttime and studied the effects of ALAN on nocturnal behavior and physiology. Very little is known about whether and how ALAN may affect the behavior of fish during subsequent diurnal periods after being exposed to ALAN.

In this paper, we used Bluegill (*Lepomis macrochirus*) as a model to test the hypothesis that exposure to ALAN at light intensities comparable to those found in artificially lit areas (i.e., 0.5, 4, and 9 lux) influences subsequent diurnal behavior assessed the following morning. We predicted that the Bluegill exposed to ALAN would be more exploratory, spend more of their time in the open, have higher locomotor activity levels, and spend more time near a novel stimulus relative to controls held in total darkness. We also predicted that there would be greater differences in their behavior when they are exposed to higher intensity lights (i.e., we would observe the greatest changes in behavior relative to the control at a light intensity of 9 lux). We chose the small freshwater teleost Bluegill as they are commonly found in shallow water near shores and docks, which makes them likely to be exposed to ALAN in nature. Moreover, they readily adapt to life in the laboratory and can therefore be handled in ways that minimize handling stressors. Given freshwater biodiversity is experiencing unprecedented losses with many emerging threats, there is a pressing need to understand the ways in which ALAN may alter fish behavior and health to develop effective mitigation and restoration strategies (Reid et al. 2019).

2 Methods

2.1 Capture and Maintenance of Study Organisms

Research occurred in eastern Ontario on Lake Opinicon at the Queen’s University Biological Station. The area is in a rural environment where there is negligible skyglow. The shoreline has a low density of cottages with some minimal dock lighting. As such, fish are rarely exposed to ALAN. Lake Opinicon is a shallow, centrarchid-dominated, mesotrophic lake. Juvenile Bluegill (average total length = 81 ±1 mm) were captured by seine netting during the day between 10:00 and 13:00 between August 17 and 24, 2019. Seine netting was chosen as it avoids potential behavioral biases associated with other capture methods such as angling (Wilson et al., 2011; Gutowsky et al., 2017). All fish were captured from similar habitat type consisting of submerged aquatic macrophytes, scattered woody debris, and soft substrate. We captured fish from similar habitat types to avoid any potential bias due to behavioral types associated with different habitat types (Kobler et al. 2011; Wolf and Weissing 2012; Lawrence et al. 2018).

Several times over a 2-week period, Bluegill was captured via seining to provide individuals for 2 days of treatments. Eighteen fish were transferred to aerated indoor holding tanks at Queens's University Biological station. The remaining fish (target was also 18) were transferred to an aerated dock tank supplied with flow-through of natural lake water, also at Queen's University Biological station, and were transferred to the indoor tanks the following day. The indoor tanks were separated into 18 equal sized partitioned sections that measured 8.5 cm by 25.5 cm. The indoor tanks were maintained on a flow-through circulation of lake water. The temperature of the water was 26 ± 0.5°C during the experiments, and oxygen levels were maintained above 95% saturation. The temperature and oxygen levels were checked immediately before and after the fish were transferred to the indoor tank, as well as the following morning before the start of the behavioral assays.

2.2 Light Treatments

We used four light treatments: (i) control (dark at night), a seasonal appropriate (based on the sunset and sunrise at the end of July in Ontario Canada) day-night rhythm of 16 h of natural sunlight and 8 h of darkness; (ii) dim light, 16 h of natural sunlight and 8 h of 0.5 lux; (ii) medium light, 16 h of natural light and 8 h of 4 lux; and (iii) a brighter treatment, 16 h of natural sunlight and 8 h of 9 lux. All brightness levels were measured by luxmeter at the surface level of the water in the chambers. We chose these light levels as they are ALAN levels that are commonly found in waterways (Moore et al. 2006; Nightingale et al. 2006; Perkin et al. 2011; Perkin et al. 2014; Kurvers et al. 2018). Due to space constraints for lighting, we ran one treatment per night (i.e., all 18 fish in the laboratory each night were exposed to the same level of ALAN). Fish were transferred into the interior tanks at 14:00 the day before they underwent behavioral trials to allow the fish to acclimatize to their tanks. The tanks were exposed to natural sunlight until sunset (no overhead lights were used during acclimatization), when all windows and doors were then covered. Two commercially available programmable LED lights (Ilumi outdoor smart bulbs) were set up 138 cm away from the tanks and 97 cm above the tanks. At sunset, the LED lights were turned on simulating the switching on of artificial lights such as dock lights. The fish were then left undisturbed until sunrise the following morning (approximately 5:30); when the lights were switched off, the windows and doors were uncovered, and the behavioral trials began. Each light treatment was repeated with the order of the trials randomized, with the exception of the second control treatment which was performed on a day when the power to the laboratory was lost.

2.3 Behavioral Trials

Our methods for behavioral assays were adapted from the methods used by Lawrence et al. (2018). Fish were transferred from their overnight holding chambers to a novel experimental tank. The behavioral arenas measured 58 cm by 40 cm, and the water depth was 20 cm with a refuge placed at one end. The refuge was composed of two artificial plants (8 cm apart) glued to a tile (20 cm by 10 cm). We had six arenas, and fish were transferred from the holding tanks to the experimental arenas randomly. All fish were released into the refuge area of the arena. A grid (2.5 cm 2.5 cm) on the bottom of the tank was used to help quantify the fish's position in the arena throughout the trial. Each tank was visually blocked from the others so fish could not see one another. GoPro Hero 3 cameras were mounted above the experimental tanks. One camera could record 2 experimental arenas simultaneously, allowing for up to 6 behavioral trials to run simultaneously. After all fish had been transferred to the experimental arena, the cameras were turned on. The behavioral tests ran for 23 min. Analysis of the videos started after 3 min to allow the Bluegill to acclimatize to the behavioral arenas. Thirteen minutes after the start of the recording (i.e., 10 min into the trial), a researcher dropped a novel object into the center of each tank to assess risk-taking behavior. The novel object consisted of an orange streamer attached to a wire, weighed down with bolts (i.e., an object that would not be encountered naturally by the fish in the wild; see below for details on video extraction). After the trials were completed, each fish was measured for length and then released back into the lake. Each fish was only used in a single trial and exposed to a single treatment (i.e., this was not a repeated measure design). Between trials, the experimental arenas were emptied and refilled with fresh lake water. These steps were repeated until all fish from the previous nocturnal holding period had completed a behavioral trial. In total, 114 fish were used: 26 for the 0.5 lux treatments, 30 for the 4 lux treatment, 26 for the 9 lux treatment, and 28 for the dark treatment. Slight differences in sample sizes among treatments arose when fish were excluded based on evidence of disease (e.g., saprolegnian fungal development) or if they escaped during transfer.

2.4 Video and Statistical Analyses

Analysis of the videos was done using Solomon coder. Activity level was recorded as the total time an individual spent swimming (Table 1). Exploration was recorded as the total time an individual spent with its entire body on the tile with the plants (Table 1). Less time in refuge would mean the individual was more exploratory. Space usage was recorded in two ways: (1) time near walls and (2) time spent in the open (Table 1). Time near wall was when an individual was within 2.5 cm of the wall or had their head pressed up against the wall. Time in the open was when an individual had the entirety of their body in the center of the tank, four squares away from walls and three away from the refuge. Time near stimulus (i.e., novel object) was recorded as time where the individual's head or body was within two squares of the base of the stimulus (Table 1). More time near the novel stimulus indicates a less risk averse individual. All data were analyzed using R (R Version 3.5.0). Statistical significance was accepted at $\alpha = 0.05$. All data is presented as the mean ± standard error unless stated otherwise (e.g., as box plots in Fig. 1). All data were analyzed with a Kruskal-Wallis test, and a Dunn's test was used as a post hoc test.

3 Results

Fish were of similar size across all treatments (Table 2; p=0.120, df=3). During the trials, Bluegill spent most of their time outside of the refuge (Table 2, Fig. 1a). However, there were no differences in exploration behavior (p=0.597, df=3) across different levels of light intensity. Bluegill in all treatments spent more time near the walls of the tank than they did in the open area (Table 2, Fig. 1b). Overall, there was no significant difference among treatments for time spent near a wall or time spent in the open (Kruskal-Wallis: p=0.578, p=0.432, respectively, df=3 for both). We did observe a significant difference in the time spent swimming among the treatments (Table 2; p=0.048, df=3, Fig. 1c). Individuals in both the 0.5 lux and the 9 lux on average swam less than fish in the dark treatment (Dunn's p=0.007 and p=0.019). Bluegill exposed to the 4 lux treatment appeared to swim less than the dark treatment, but this was not significantly different (Dunn's p=0.170). In general, the Bluegill did not spend much time near the novel stimulus (Table 2, Fig. 1d), and there was no significant difference in time spent near the novel stimulus across treatments (Kruskal-Wallis: p=0.353, df=3).

4 Discussion

In the wild, fish often use refuges in an attempt to reduce predation risk (Sih 1997). Therefore, a decrease of time spent in a refuge area could increase the risk of predation for Bluegills. Indeed, Bluegills have been shown to use refuge patches as protection from predators and will reduce movement between patches in the presence of predators (Gotceitas and Colgan 1990). Predators such as the

Table 1 Defining the behavioral metrics studied and their potential ecological effects

Behavioral metric	What was measured	Ecological significance
Activity levels	Time spent swimming	Changing activity levels will change foraging frequency (Boisclair and Leggett 1989) and predation risk (Gotceitas and Colgan 1990)
Space usage	Time spent near wall Time spent in open	Changes in time spent in different areas will change anti predator behavior (Werner et al. 1981), foraging success (Ehlinger and Wilson 1988), and risk of predation (Chipps et al. 2004)
Exploration	Time spent in refuge	Changing exploration levels can affect foraging success (Eliassen et al., 2007) and predation risk (Chipps et al. 2004)
Risk aversion	Time spent near novel stimulus	A decrease in risk aversion could increase the likelihood of predation (Hulthén et al. 2017)

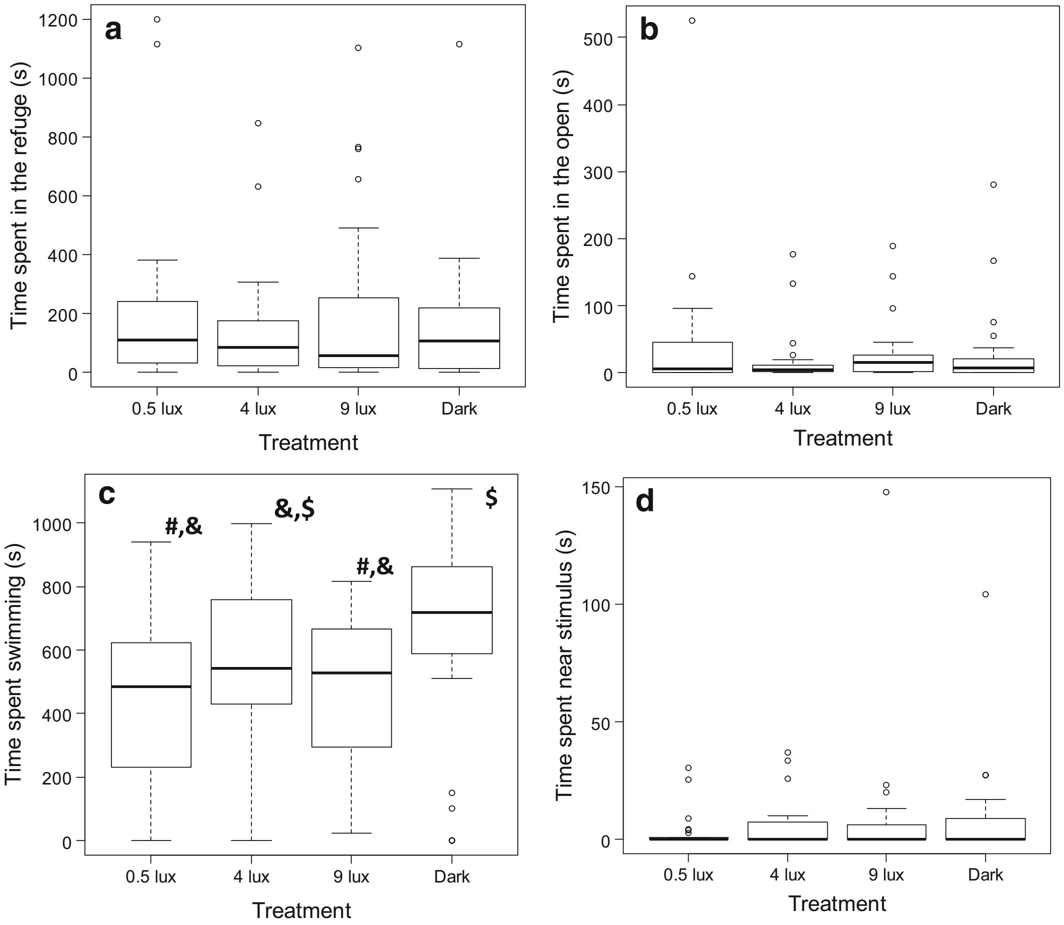

Fig. 1 The effects of the ALAN treatments on **a** exploration, **b** space usage, **c** activity level, and **d** risk. Statistical differences are noted by dissimilar symbols (only on panel **c**). All figures (box plots) were plotted with a 95% confidence interval, and statistical outliers are represented by the clear dots. Statistical significance was accepted at α=0.05

Largemouth Bass have also been shown to have higher success in capturing Bluegills in open water as opposed to in refuge patches (Chipps et al. 2004). We predicted that Bluegills exposed to ALAN would spend more time exploring during the behavioral trials, resulting in less time in the refuge. In our study, we did not find any consistent increase or decrease in exploration behavior across individuals in the ALAN treatments. The small changes found

Table 2 The mean, standard error and *p* value of each treatment per behavioral test

Behavioral trial	0.5 lux	4 lux	9 lux	Dark	*p*	*F*
Sample size	26	30	26	28		
Average size (cm)	8.0 ± 0.2	8.0 ± 0.1	8.4 ± 0.2	8.0 ± 0.1	0.120	5.83
Exploration: time spent in refuge (s)	207 ± 59	132 ± 33	209 ± 57	154 ± 35	0.597	2.77
Space usage: time near wall (s)	659 ± 82	877 ± 51	680 ± 62	689 ± 72	0.916	6.58
Time in open (s)	44 ± 20	17 ± 7	27 ± 9	27 ± 11	0.432	2.02
Activity level: time spent swimming (s)	455± 53	557 ± 50	485 ± 47	635 ± 63	**0.048**	9.57
Risk: time spent near novel stimulus (s)	3.0 ± 1.5	5.1 ± 1.7	9.6±5.5	8.5 ± 3.7	0.353	3.76

Bolded values are significant at an α=0.05

between any ALAN treatment and the dark control treatment were not statistically significant indicating that at the brightness tested, ALAN did not influence the exploratory behavior of Bluegill.

Other aspects of space use can yield information on fish responses to different conditions. While Bluegills are capable of living and foraging in both littoral and open areas (Ehlinger and Wilson, 1988), they have been shown to specialize in one of the two area types (Werner et al. 1981). Bluegills have anti-predator defenses for both areas, but common predators such as the Largemouth Bass have been shown to be more effective at hunting Bluegills in open areas (Chipps et al. 2004). As the Bluegills used in this experiment were collected from sites with dispersed woody debris and short vegetation, more time spent in the open would presumably increase their predation rate. We predicted that Bluegills in the ALAN treatments would spend more time in the open areas of the behavioral tanks than the dark control treatment. However, our findings revealed that space usage in Bluegills was not affected by ALAN at the brightness tested here.

It is well known that the extent of locomotor activity is influenced by a variety of biotic and abiotic factors (Scherer 1992; Cooke et al. 2004) and is thus commonly used as a means to assess how fish respond to external cues (or pollutants) such as ALAN (e.g., Scott and Sloman 2004; Foster et al. 2016; Pulgar et al. 2019). We predicted that individuals exposed to ALAN would have increased locomotor activity levels the following morning. In contrast, we found that swimming decreased on average for all ALAN treatments compared to the dark control group. Individuals in both the 0.5 lux and the 9 lux treatments swam significantly less than individuals in the dark control treatment. This was surprising as it is the opposite effect to what has been previously observed. Pulgar et al. (2019) reported an increase in both swimming activity and metabolic activity in the intertidal rockfish (*Girella laevifrons*) during the day after they were exposed to ALAN overnight. A potential explanation for the decrease in swimming activity during the day in our studies would be that Bluegill in the ALAN treatments exhibited elevated swimming levels at night. Bluegill sunfish are diurnal fish and typically between 68 and 75% of their activity occurs during the day, allowing for them to rest for most of the night (Reynolds and Casterlin 1976). However, in the presence of ALAN, other foraging fish have been shown to increase foraging activities (Czarnecka et al. 2019). In the Pulgar et al. (2019) study, the fish were exposed to a much brighter ALAN (70 lux) and were exposed to ALAN for 10 days. It is possible that brighter ALAN or a longer exposure could lead to more or even less swimming. The evidence base on how light affects fish remains limited, so it remains difficult to know the specific contexts in which light alters behavior and in which ways.

Past research has shown that ALAN can disrupt some of the processes involved in risk taking (Kurvers et al., 2018), which could increase the risk of predation. We predicted that Bluegill exposed to ALAN would be less risk averse, so they would spend more time near a novel stimulus. We did not find any common trend across individuals in the ALAN treatments. Our results indicate that ALAN at the brightness tested does not influence risk aversion of Bluegills. We also predicted that the magnitude in behavioral alterations relative to controls (fish held in total darkness at night) would be least for the lowest ALAN treatment and highest for fish exposed to the brightest ALAN treatment. We did not find any trends indicating that the brightness of the ALAN had any effect on the relative level of behavioral alteration relative to controls. The light intensities chosen are of ecological relevance as they are within the common light intensities found near waterways (Moore et al. 2006; Nightingale et al. 2006; Perkin et al. 2011; Perkin et al. 2014; Kurvers et al. 2018). They are however much lower than the intensities used in previous research which in some cases included brightness levels of 70 lux (Pulgar et al. 2019) up to 500 lux (Kurvers et al. 2018). It is possible that the behavioral alterations observed here would be magnified if different light intensities were used; however, we aimed to limit our experimental design to only include ecologically relevant light intensities.

To conclude, most of the behaviors measured here during the day were not influenced by whether fish were exposed to ALAN the previous night. However, we did find a significant reduction in the locomotor activity of Bluegill that were exposed to ALAN at light levels that are environmentally relevant. This reduction was recorded at light levels as low as 0.5 lux. Around 18.7% of the global land area (Cinzano et al. 2001; Gaston et al. 2015) and 22% of the world's coastal regions (Davies et al. 2014; Davies and Smyth 2018) are exposed to some form of ALAN of a brightness of 0.5 lux or greater (Kyba et al. 2017b). While the water-air barrier may be enough to prevent skyglow from being bright enough to currently affect multiple aspects of Bluegill behavior, it is increasing in brightness (Kyba et al. 2017a) and may reach an intensity sufficient to cause other behavioral or biological changes in the future. Decreasing the time spent, swimming during the day may influence risk of predation (Gotceitas and Colgan 1990; Pitcher and Soluk 2016), and this potentially could modify predator-prey interactions (Dewey et al. 1997). This is one of the first studies to assess the effects of ALAN on freshwater fish and one of the few to assess the effects of ALAN on the subsequent diurnal behavior of fish. We encourage additional research to better understand the ecological impacts of ALAN on aquatic organisms such as fish.

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