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Ontogeny of light avoidance in juvenile lake sturgeon

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Abstract

Hatchery-reared age 1+ and 4+ lake sturgeon (*Acipenser fulvescens*) were assayed to determine the effectiveness of coloured, strobing LED light guidance device (LGD) at achieving behavioural guidance for attraction or avoidance responses. Based on an initial y-maze dichotomous choice study in age 1+ fish during daytime, we selected green, blue, orange, and full-spectrum white light, all strobing at 1 Hz, for further testing. During nighttime light guidance trials, age 1+ sturgeon demonstrated the fastest entries and greatest proportion of entries to the cone of illumination in the experimental raceway when the LGD was producing blue light, and the lowest proportion of entries in response to orange light. Conversely, they also spent the greatest amounts of time under illumination during orange light trials. Blue light was associated with the greatest proportion and total numbers of complete passages through the illuminated zone, although passage rates through this area were observed during the unilluminated control trials. White light resulted in the least time spent in the illuminated zone, and the lowest rates of passage. Under the nighttime testing scenario, the age 4+ sturgeon, by contrast, demonstrated strong avoidance of blue light and white light. While their behaviour was negatively phototactic in general, orange light was the least repulsive. For the behavioural guidance of lake sturgeon moving at night, we recommend the use of blue light strobing at 1 Hz for the attraction of the 1+ age class and white light strobing at 1 Hz for their repulsion. For age 4+ fish, we recommend the use of blue light or white light strobing at 1 Hz for repulsion and caution that (a) light as a behavioural guidance tool appears most effective as a repulsive stimulus, and (b) further testing under both laboratory and field conditions are required.

1 | INTRODUCTION

Physical barriers in waterways, including hydroelectric dams, create a number of challenges for aquatic organisms, particularly as they relate to connectivity (Calles & Greenberg, 2009; Pringle, 2003; Vörösmarty et al., 2010). Entrainment of fish (either resident or migratory species) through water intake structures and resulting injury or mortality (Barnthouse, 2013) has direct negative impacts on population abundance, often during critical life-history phases associated with migrations (Auer, 1996; Baril, Buszkiewicz, Biron, Phelps, & Grant, 2017; Kynard & Horgan, 2002). Attempts to mitigate entrainment (e.g. through the installation of louver arrays (Ford et al., 2017) or bar racks (Amaral, 2003; Amaral, Cain, Black, & McMahon, 2001; Kynard & Horgan, 2001), may permit the passage of smaller individuals (Coutant & Whitney, 2000), while creating a risk of impingement on the structures for larger fish (Patrick, Mason, Powell, Milne, & Poulton, 2014). A method to prevent fish from coming into contact with hazards in the first place would be a marked improvement.

Non-physical barriers consisting of sensory stimuli, including acoustic signals, bubble curtains, and light (Coutant, 1999, 2001;

Goetz, Dawson, Shaw, & Dillon, 2001; Maiolie, Harryman, & Ament, 2001; Perry et al., 2014), have all been tested in reducing rates of entrainment and impingement near turbines and barriers, with varying degrees of success. The use of coloured light, designed to match the retinal sensitivities of target species, has only recently been explored (Elvidge et al., 2018; Ford et al., 2017, 2018 ; Sullivan et al., 2016) using LED-based technology capable of emitting different spectra. In the case of juvenile (0+) white sturgeon (*Acipenser transmontanus*), green light matching the peak absorbance of the retinal photopigments in both rod cells and one type of cone cell (Loew & Sillman, 1993; Sillman, Sorsky, & Loew, 1995; Sillman, Spanfelner, & Loew, 1990), elicited the greatest levels of attraction under laboratory conditions. The same technology also has the advantage of strobing at programmable frequencies; for example, juvenile white sturgeon demonstrated greater attraction to green light strobing at 20 Hz than they did to green light strobing at 1 Hz (Ford et al., 2018).

Here, we present the results of a study on the attraction or avoidance to different colours and strobe rates of LED light in two age classes (1+ and 4+) of captive-bred lake sturgeon (*A. fulvescens*) of wild provenance. We focus on lake sturgeon as they are designated as at risk in Canada due to habitat fragmentation, amongst other causes (COSEWIC, 2007), and they frequently inhabit areas favoured by hydroelectric development (Haxton & Cano, 2016). Consequently, there is great interest in mitigating entrainment given their status in many regions (Haxton, Sulak, & Hildebrand, 2016). Previous examinations of lake sturgeon retinas have found three types of cone cell and one type of rod cell, with the latter comprising ~70% of retinal cells (Sillman, Ong, & Loew, 2007). The visual pigment of the rod cells has mean peak absorbance at 541 ± 2 nm, while the pigments of the three cone cells have peak absorbances at 619 ± 3 nm, 538 ± 1 nm, and 448 ± 1 nm (Sillman et al., 2007). Based on these findings, we selected blue (448 nm), green (538 nm), orange (619 nm), and full-spectrum white LED light as behavioural guidance stimuli. In a recent study examining the effectiveness of coloured LED light on behavioural guidance of juvenile white sturgeon, a strobe rate of 1 Hz elicited the strongest responses in focal fish, while no differences in response to constant light output or light strobing at 20 Hz suggested that a strobe rate of 20 Hz may have exceeded critical flicker frequency (CFF) and was indistinguishable from constant light (Ford et al., 2018). Consequently, we exposed age 1+ lake sturgeon to dichotomous choice tests of either constant light or strobe rates of 1 Hz or 10 Hz to inform our selection of light stimuli for a second behavioural guidance experimental component in an open-field test.

2 | MATERIALS AND METHODS

2.1 | Trial arena and test fish

We conducted this experiment at the Grand Rapids Fish Hatchery (GRFH; owned and operated by Manitoba Hydro) in Grand Rapids, MB, Canada, during August 2017. Test fish were captive-bred age 1+ (from broodstock collected in Landing River, upper Nelson River basin) and age 4+ (from broodstock collected in Birthday Rapids, lower Nelson River basin) lake sturgeon from the Keeyask Hydropower Limited Partnership conservation stocking program (KHLP, 2015). The age classes are held separately to prevent disease and parasite transmission between different groups in circular, flow-through rearing tanks supplied with unfiltered Saskatchewan River water drawn from the forebay of the Grand Rapids generating station. The tanks are supplied with water in a counter-clockwise direction of flow (i.e. the sturgeon continuously swim to their left). The hatchery is equipped with six outdoor raceways measuring 25.5 m × 1.84 m × 1.5 m (L × W × D), divisible into thirds (8.5 m length) via metal screens that fit into grooves in the concrete sides of the channels. The raceways were also supplied with unfiltered river water at rates of ~500 L/min and filled to depths of 0.6 m (total volume at one time ≈28 200 L). The 8.5 m sections furthest from the water inputs in each of two adjacent raceways (Figure 1a) were partitioned off as trial arenas, to avoid having to decontaminate the trial arena between age classes as per hatchery biosecurity protocols.

2.2 | Light guidance device and rgb saturations

The LED-based light guidance device (LGD; ATET-Tech, Inc., Thornhill, ON; www.atet-tech.com) used has computer-programmable colour output based on manipulating percentage RGB (red-green-blue) saturations (i.e. white light is 100-100-100). The LGD is equipped with integrated temperature and turbidity probes and these values are recorded when the device is connected to a control computer. We converted wavelength to RGB saturation using an online converter (https://academo.org/demos/wavelength-to-colour-relationship/; values from the converter range from 0 to 255, so we calculated percentage saturations as follows: x ÷ 255 × 100%), with the following results: white (full spectrum; 100-100-100), blue (448 nm; 0-23-100), green (538 nm; 50-100-0), and orange (619 nm; 100-48-0).

2.3 | Experimental protocol

2.3.1 | Colour and strobe preferences in age 1+ lake sturgeon

All available 1+ lake sturgeon (N = 252) were exposed to one of 13 LGD settings (blue, green, orange, or white light, at 1 Hz, 10 Hz, or constant output, or an unilluminated control treatment; all N = 19–20) in y-maze dichotomous choice tests under daytime conditions. Daytime conditions were selected to test colour and strobe preferences as acclimation to high ambient light levels relies on colour vision via the retinal cone cells and precludes general phototactic attraction to the light stimuli from stimulation of the rod cells that are the basis for vision in low-light conditions (Fang et al., 2004). The y-maze was constructed out of one 2.44 m × 1.22 m × 0.5 cm (length × height × width) panel of dark grey PVC sheeting placed to bisect one end of the 8.5 m arena, and the LGD was placed into the center of either 2.44 m wing of the y-maze with their light cone aimed towards the far end of the arena. Individual age 1+ sturgeon were placed into the arena at the end opposite the y-maze with the LGD operating, and their immediate movements were recorded. Trials ended when the focal fish first entered either side of the y-maze, after which the PIT tags were recorded, and the fish was measured, weighed, and returned to net pens placed in the

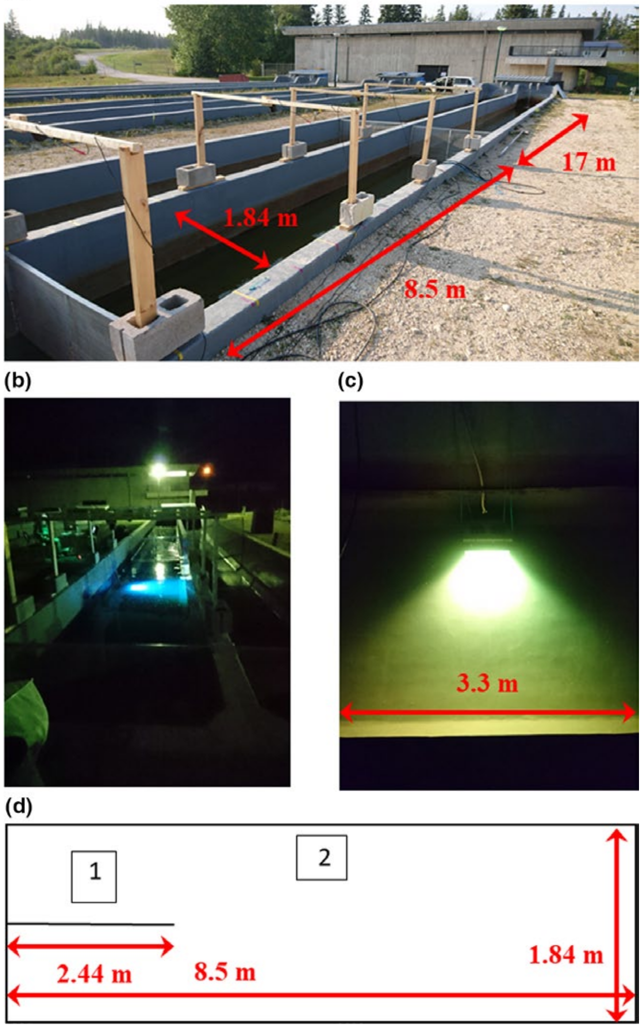

FIGURE 1 Experimental setup and trial arena at the Grand Rapids Fish Hatchery. (a) Trial arena: one-third (8.5 m) of a raceway (25.5 m × 1.84 m) was partitioned off using metal screens and filled to a depth of 0.6 m. Four infrared security cameras were suspended overhead on wooden u-frame scaffolds. (b) Trial arena at night, with ambient background lighting from the hatchery building and the LGD producing blue light. (c) Overhead view of the cone of illumination (3.3 m long on the opposite wall) produced by the LGD (green light) at night. (d) Schematic diagram of both the removable y-maze partition with a 2.44 m long PVC sheet at one end of the trial arena for dichotomous choice testing. Box 1 illustrates the position of the LGD during dichotomous choice testing and box 2 illustrates its position during the open-field testing

original holding tanks to prevent re-testing individuals. The LGD was moved between sides of the y-maze (Figure 1d) following each replicate block (N = 13 trials per block), and data from the control trials (no light stimulus) were used to test for the presence of inherent side bias.

2.3.2 | Behavioural guidance in an open field

Under night conditions (22:00–03:00), the LGD was positioned at the midpoint of the long axis of the arena against one side wall (Figure 1b), creating a cone of light in the center of the arena that extended 3.3 m on the opposite wall (Figure 1c). We released the fish at one end of the arena and observed them for 5 min using an infrared security camera array (four PRO-642 camera units connected to a DVR9-4200 9 Channel 960H Digital Video Recorder; Swann Communications U.S.A Inc., Santa Fe Springs, CA) suspended above the trial arena. During the trials, we recorded whether each fish entered the illuminated area in the middle of the arena; the latency to enter the illumination; number of entries to and exits from the illuminated area; whether or not the fish passed all the way through the illuminated area to the opposite end of the arena; and total times spent inside and outside the illuminated area.

Five experimental treatments consisted of blue, green, orange, and white light, all strobing at 1 Hz, as well as an unilluminated control, based on the findings of the y-maze preference study. We used a subset (N = 100 total; N = 20 per treatment) of the age 1+ sturgeon tested in the y-maze, and all available (N = 35; N = 7 control, N = 8 blue; N = 7 green; N = 6 orange; N = 7 white) age 4+ sturgeon. After each trial, the PIT tag of the focal fish was recorded, and age 1+ plus were returned to their holding tanks while age 4+ fish were measured, weighed, and returned to their holding tank.

TABLE 1 Odds and odds ratios of LGD approaches by age 1+ lake sturgeon in response to different colours and strobe rates of LED light

Treatment			
Colour	Strobe	Odds	Odds ratio (relative to control)
Control		2.333	–
Blue	1 Hz	1.111	0.476
	10 Hz	0.727	0.312
	Constant	0.667	0.286
Green	1 Hz	1.222	0.524
	10 Hz	0.583	0.249
	Constant	0.727	0.312
Orange	1 Hz	0.727	0.312
	10 Hz	0.333	0.143
	Constant	0.727	0.312
White	1 Hz	0.583	0.249
	10 Hz	1.500	0.643
	Constant	0.727	0.312

2.4 | Statistical analyses

2.4.1 | Preferences in age 1+ lake sturgeon

Whether or not a focal fish first entered the side of the y-maze containing the LGD was scored in binary (1 = LGD first; 0 = non-LGD side first). This binary response was then analyzed in a logistic regression with treatment (LGD setting) and side (LGD on the left or right) as fixed-effects factors, and body condition index (100 × (Mass · L^{-3}), with mass in g and total length in cm), temperature (°C), and turbidity (FTU) as linear covariates against a binomial

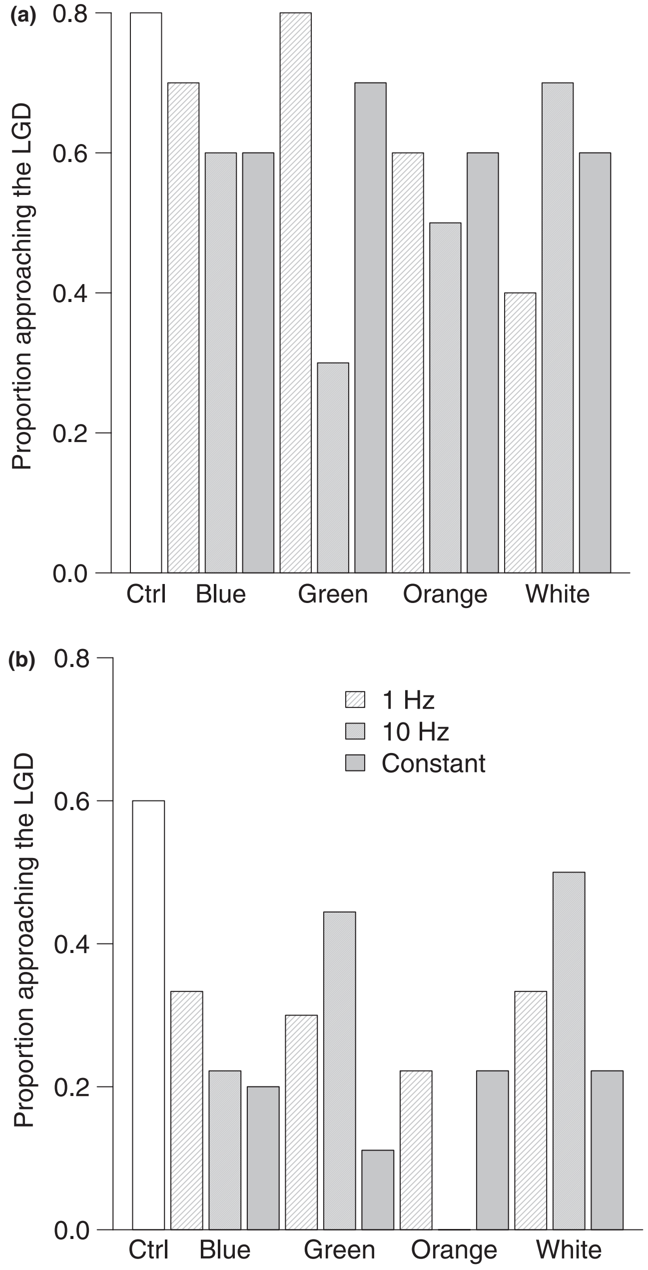

FIGURE 2 Proportion of age 1+ lake sturgeon initially approaching the LGD when it was on (a) the left side or (b) the right side of the trial arena under daytime conditions. Strobe rates of coloured LED light are given within the bars

distribution. Frequency of entries to each side in all treatments, as well frequency of entries to the side containing the LGD, were extracted from the data to identify potential side bias. We examined preferences for specific colour and wavelengths using odds ratio testing with the control trials serving as a baseline.

2.4.2 | Light guidance trials

All data were analyzed as generalized linear models with treatment (LGD setting) and side (LGD on the left or right) as fixed-effects factors, and body condition index (as above), temperature (°C), and turbidity (FTU) as linear covariates. Data were analyzed against either Gaussian distributions with *F*-tests (latency to enter the light cone (s), time spent in the light cone [s]), binomial distributions with likelihood-ratio χ^2 tests (i.e. logistic regressions: whether or not a fish entered the light cone; whether or not a fish passed entirely through the light cone), or Poisson distributions with likelihood-ratio χ^2 tests (number of entries into the light cone; number of complete passages through the light cone). Fish that did not enter the illuminated area or either side of the y-maze were assigned latencies to enter of 300 s. Age 1+ and 4+ fish were analyzed separately to remove life history differences in response patterns as confounding variables. All analyses and figures were produced using R version 3.4.2 (R Core Team, 2017) and the "car" (Fox & Weisberg, 2011) and "gplots" (Warnes et al., 2016) packages. Complete statistical results are provided as Supporting Information.

3 | RESULTS

3.1 | Colour and strobe preferences

We found significant evidence of side-bias, with 60% of the age 1+ sturgeon entering the left side of the y-maze during control trials (12 out of 20 trials). Overall, 65.9% of trials resulted in the age 1+ sturgeon entering the left side (166 out of 252 trials; $\chi^2_1 = 26.62$, $p < 0.001$), regardless of where the LGD was positioned. The age 1+ sturgeon were generally more likely to enter the control (no LGD) side (138 out of 252 trials) than they were the LGD side (114 out of 252 trials), independent of LGD setting. There were no statistically significant effects of LGD treatment, body condition, temperature, or turbidity on probability of entering the LGD side first (Table S1). Furthermore, no age 1+ sturgeon approached the LGD when it was on the right side of the y-maze and producing orange light at 10 Hz.

Age 1+ lake sturgeon had the greatest odds of first entering the side containing the LGD during the control treatment trials (Table 1), followed by white light strobing at 10 Hz and green light strobing at 1 Hz, independent of side bias. However, when odds ratios (odds for a given treatment divided by odds for the control) are considered, a strobe rate of 1 Hz was associated with the highest odds of initial entry to the LGD side for three out of the four colours tested (blue, green, orange).

When assessing the proportion of first entries on the side containing the LGD (i.e. accounting for side bias), green light strobing at 1 Hz and the control treatment both had the highest proportion of first entries when the LGD was on the left side of the y-maze (Figure 2a), while the control treatment had the highest proportion of first entries when the LGD was on the right side of the y-maze (Figure 2b). Based on these observations, we selected the 1 Hz strobe rate for subsequent light guidance trials.3.1.1 | Light guidance trials

The proportion of age 1 + sturgeon entering the cone of illumination was significantly influenced by side ($\chi^2_1 = 7.73$, $p = 0.03$), but not by LGD treatment, body condition, temperature, or turbidity (Table S2), with the greatest proportion of entries during blue light trials (Figure 3a). There were no effects of LGD treatment, side, body condition, or turbidity (Table S3) on the number of entries into the cone of illumination by individual sturgeon (Figure 3b), but there were significant effects

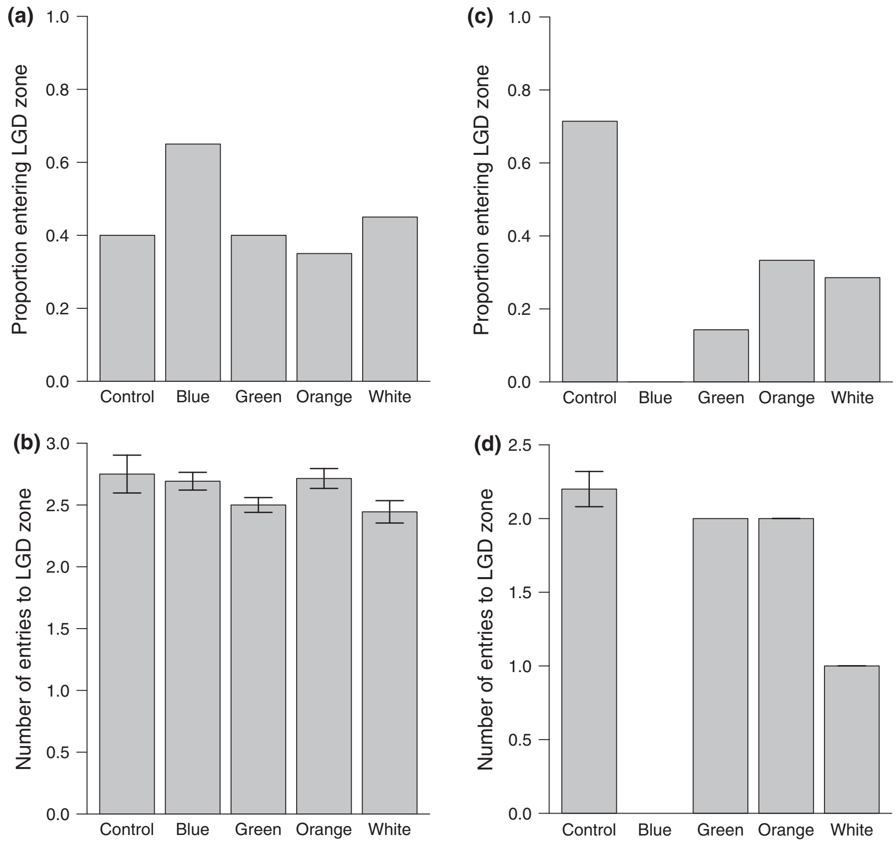

FIGURE 3 (a, c) Proportions of age 1+ and 4+ lake sturgeon, respectively, entering the light cone, and (b, d) mean (±SE) numbers of entries to the light cone under night conditions

of temperature ($\chi^2_1 = 4.24$, $p = 0.04$) and an interaction between LGD treatment and side ($\chi^2_1 = 11.85$, $p = 0.02$). The correlation between temperature and number of entries was positive, but not statistically significant when examined separately (Pearson's $r = 0.153$, $p = 0.13$).

Age 1+ lake sturgeon took significantly less time (shorter latency) to enter the cone of illumination when the LGD was placed against the left side of the raceway (mean latency 192.5 s vs. 223.5 s; $F_{1,31} = 4.25$, $p = 0.048$), and there were no significant effects of LGD treatment, body condition, temperature, or turbidity (Table S4). Shortest mean latencies to enter the cone of illumination were recorded during blue and orange light treatments (Figure 4a). Although there was no overall effect of LGD treatment or any other factors (Table S3), time spent in the cone of illumination was greatest during the orange light trials and shortest during the control and white light trials (Figure 4b).

The greatest proportions (Figure 5a) and mean total numbers of complete passes through the cone of illumination (Figure 5b) for age 1+ sturgeon occurred during the control trials, followed by the blue light at 1 Hz trials. White light trials were associated with the lowest rates and numbers of passages. While there were no statistically significant trends in rates of passage (Table S6), LGD treatment did differ in total numbers of passages ($\chi^2_4 = 12.99$, $p = 0.011$; Table S7). Temperature and turbidity were excluded from this last model due to the low overall occurrence of multiple passes and resulting loss of degrees of freedom.

The proportion of age 4+ sturgeon entering the cone of illumination was significantly influenced by LGD treatment ($\chi^2_4 = 11.39$, $p = 0.023$), but not by any other model terms (Table S8), with the greatest proportion of entries occurring during the control and orange light trials, and the fewest during the green light trials, with little difference between orange and white and no entries during blue light trials (Figure 3c). The number of entries into the illuminated zone was significantly influenced by LGD treatment ($\chi^2_4 = 18.73$, $p < 0.001$), but not by any of the other variables (Table S9). Apart from the control trials, green light and orange light resulted in the greatest mean numbers of entries by individual fish (by $N = 1$ and 2 fish, respectively), and white light the least (by $N = 2$ fish). No sturgeon entered during blue light trials (Figure 3d).

The other responses of the age 4+ sturgeon to the light stimuli differed markedly from those of the age 1+ sturgeon, particularly at blue light strobing at 1 Hz. Latency to enter the cone of illumination was not significantly influenced by LGD setting or any other model term (Table S10). The shortest and longest latencies to enter occurred during the orange and white light trials, respectively. No age 4+ sturgeon entered the cone of illumination during blue light trials and only one fish entered the illuminated area during green light trials (Figure 4c). There were also no significant explanatory variables in relation to time spent in the illuminated zone (Table S11), although the greatest time spent in the illuminated zone, apart from the control treatment, was by the single fish that entered during the green light trials, and the shortest time spent was during the white light trials (Figure 4d).

The only trials during which age 4+ lake sturgeon passed entirely through the illuminated zone were during the control trials, and only two fish demonstrated this behaviour (Figure 5c). While

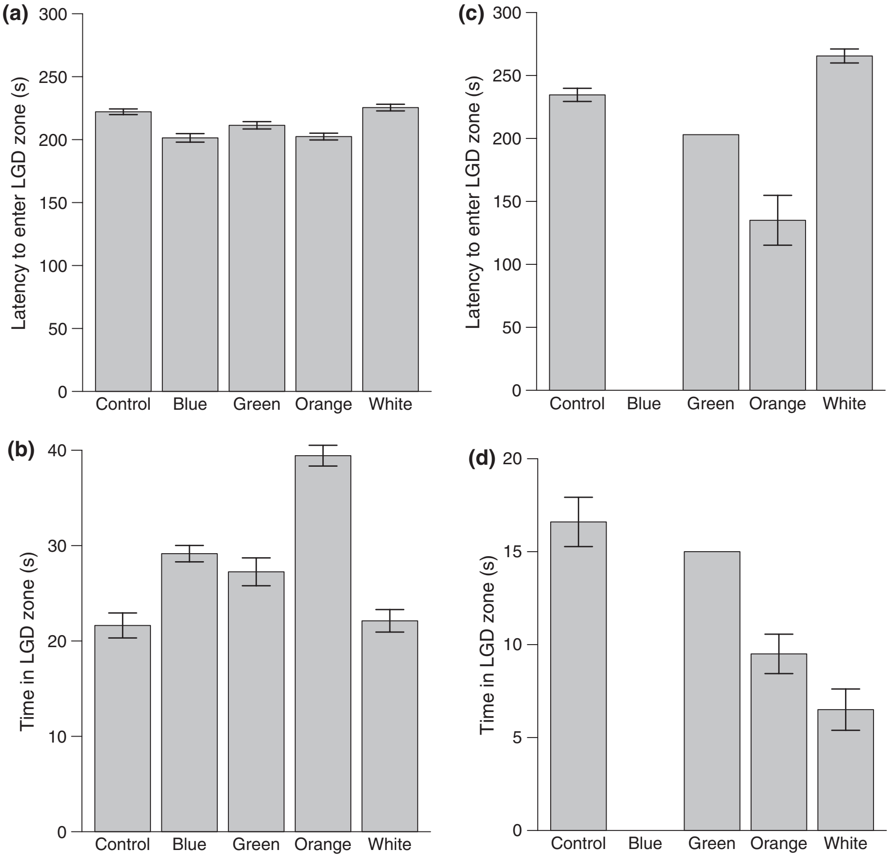

FIGURE 4 Mean (±SE) times (s) (a, c) to enter the light cone and (b, d) spent in the light cone during 5 min trials in age 1+ and age 4+ lake sturgeon, respectively, under night conditions

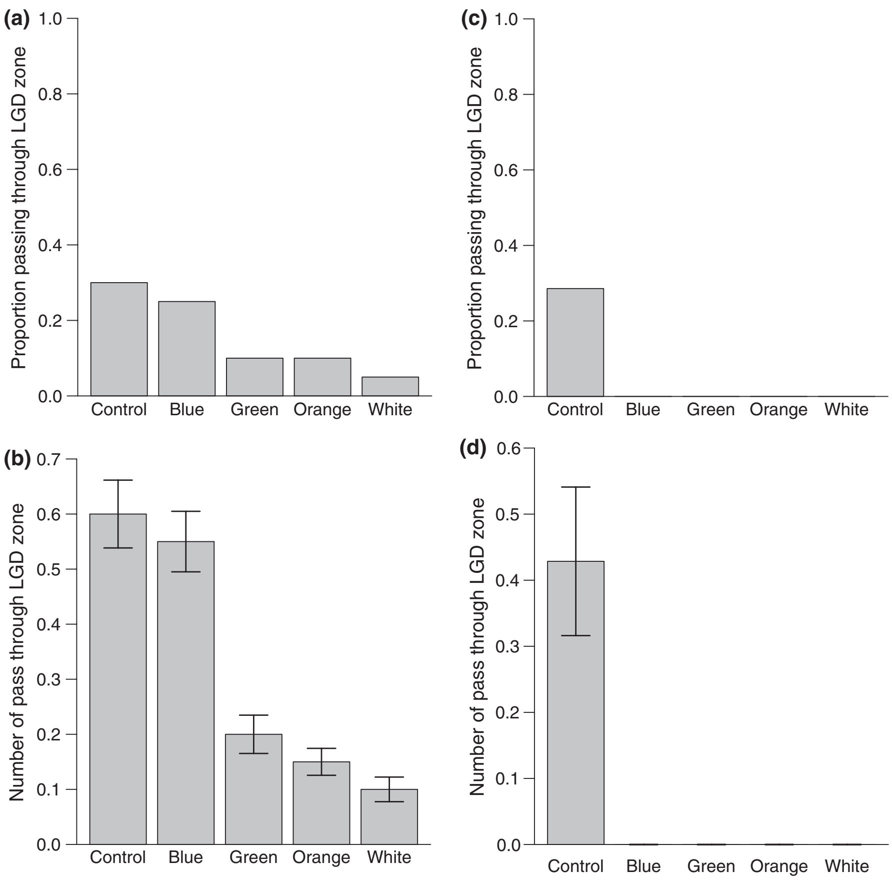

FIGURE 5 (a, b) Proportions of age 1+ and age 4+ lake sturgeon, respectively, passing through the light cone, and (b, d) mean (±SE) numbers of complete passages through the light cone under night conditions

there was a significant effect of LGD treatment on whether or not an age 4+ sturgeon passed through the illuminated zone ($\chi^2_4 = 11.24$, $p = 0.024$), there were no effects of side or body condition (Table S12). There were no effects of any variable on the number of passages (Figure 5d; Table S13). Temperature and turbidity were excluded from these analyses due to the low number of passages observed and resulting loss of degrees of freedom.

4 | DISCUSSION

The responses of the age 1+ lake sturgeon in our study to the different light stimuli were equivocal and did not differ from the control treatment under nighttime conditions in experimental settings. Conversely, age 4+ lake sturgeon demonstrated consistent negative phototaxis, and were most repelled by blue light strobing at 1 Hz. This is experimental evidence for the ontogeny of blue light avoidance in lake sturgeon; however, to our knowledge, ontogenetic development of blue-light sensitivity has not been demonstrated in this species (but see Rodriguez & Gisbert, 2002 for a description of this development in Siberian sturgeon *A. baerii*).

The left-biased movements we observed in age 1+ sturgeon in the preference study are more likely the result of inherent side bias in their swimming movements than they were of any effects of light stimulus. While we did not test directly for the presence of behavioural lateralization in this population of sturgeon (Bisazza, Facchin, & Vallortigara, 2000), nor directly examine whether or not environmental factors had shaped this tendency (e.g. Domenici, Allan, McCormick, & Munday, 2011), the consistent positive rheotaxis we observed in the fish in the circular holding tanks with constant counter-clockwise flow may have been the underlying cause of the side bias. Hatchery-reared sturgeon intended for use in experimentation may therefore benefit from having the direction of circular flow reversed periodically.

For the behavioural guidance of lake sturgeon, our findings suggest that the use of blue light strobing at 1 Hz may be ineffective for the repulsion of the 1+ age class, while white light strobing at 1 Hz tends to elicit repulsion. For age 4+ fish, our findings suggest that the use of blue light or white light strobing at 1 Hz is effective for repulsion but we observed this age class to be negatively phototactic, in general. However, these observations are based on relatively small sample sizes ($N = 20$ per treatment for the 1+ fish, and $N = 6–8$ for the 4+ fish), so additional lab- and field-based studies are required to verify these findings. In northern Manitoba, lake sturgeon do not reach sexual maturity before 15+ years of age (COSEWIC, 2007), so future studies should aim to include adult fish that undergo spawning migrations (Auer, 1996; Birstein, Bemis, & Waldman, 1997; McCabe & Tracy, 1994; Parsley, Popoff, Wright, & Leeuw, 2008). Nevertheless, sturgeon of all life-history stages, including out-migrating juveniles, may also be vulnerable to entrainment. Knowledge of ontogenetic differences in movement patterns specific to different reservoirs would be valuable for informing targeted, localized guidance strategies. In general, we recommend that guidance strategies should focus on using repellant stimuli to reduce encounters with hazards and resulting sturgeon mortality.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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