Title

Prey group cohesion mediates the outcome of predator—prey interactions under artificial lighting

Journal

Functional Ecology

ISSN

0269-8463

Authors

Frey, Jessica R

Burford, Benjamin P

Robinson, Rebecca R

et al.

Publication Date

2026-06-28

DOI

10.1111/1365-2435.70389

Received: 17 October 2025 | Accepted: 17 May 2026

DOI: 10.1111/1365-2435.70389

Functional Ecology

RESEARCH ARTICLE

Prey group cohesion mediates the outcome of predator–prey interactions under artificial lighting

Jessica R. Frey | Benjamin P. Burford | Rebecca R. Robinson | Lance K. Takata | Brendan M. Lehman | Cyril J. Michel

Fisheries Collaborative, Program Affiliated With Fisheries Ecology Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Institute of Marine Sciences, University of California, Santa Cruz, Santa Cruz, California, USA

Correspondence
Jessica R. Frey
Email: jefrey@ucsc.edu

Handling Editor: Anthony Herrel

Abstract

1. The highest rates of piscivorous predation in the field have been recorded during crepuscular light levels associated with sunrise and sunset or artificial lighting at night (ALAN). Hypothetically, this occurs because, under low-light conditions, prey lose the ability to visually sense and evade approaching predators, while predators maintain the ability to visually sense and attack prey. However, many prey fishes form social groups, where visually sensing and responding to one another is a key component of anti-predator behaviours. Thus, for social prey, higher rates of predation under crepuscular conditions could additionally involve the deterioration of prey group behaviours with diminishing light.
2. We conducted a laboratory study exposing groups of predator-naïve, hatchery-raised juvenile rainbow trout (*Oncorhynchus mykiss*) to natural-origin piscivorous largemouth bass (*Micropterus salmoides*) under one of three light treatments: 'high'—representative of brighter crepuscular periods or direct ALAN illumination, 'medium'—dimmer crepuscular periods or sky glow from ALAN, or 'low'—night or no ALAN. We then statistically evaluated potential associations between light treatment, prey group cohesion and predator activity.
3. Under the high treatment, prey groups were most cohesive, predators attacked prey most frequently, and attacks were least likely to be successful. Under the medium treatment, prey group cohesion began to deteriorate, and attacks were most likely to be successful. Under the low treatment, prey groups were least cohesive and predators were least active. Across all light treatments, the less cohesive the prey groups were, the higher the probability that interested predators would attack, and that such attacks would result in prey being consumed.
4. Our results suggest that outcomes from interactions between piscivorous predators and social prey could depend more on prey group cohesion, and how this changes with light level, than on the light level itself. This could be relevant for current mechanistic models of foraging, where a predator's ability to

Jessica R. Frey and Benjamin P. Burford contributed equally and share first authorship.

successfully consume prey depends more on physical conditions, such as light level, than on biotic conditions, such as prey density. Incorporating the effects of social behaviour into mechanistic models could therefore help resolve the impacts of ALAN on imperilled fishes and prioritize relevant restoration efforts.

KEYWORDS
artificial light at night (ALAN), crepuscular predation, piscivorous predation, predation risk, predator–prey interactions, prey group cohesion

1 | INTRODUCTION

In the field, piscivorous predation is highest under light levels associated with crepuscular periods (Cerri, 1983; Linehan et al., 2001; Olmsted, 1974). A common explanation is that predation is limited during the day by the prey's increased ability to visually sense and respond to larger-bodied predators (Breck, 1993) and at night by the predator's decreased ability to visually sense and respond to smaller-bodied prey (McMahon & Holanov, 1995). This explanation is supported by two central observations. First, reaction distances of fishes respond asymptotically to light level, with the magnitude of the response saturating at higher light levels and rapidly diminishing at lower light levels (Howick & O'Brien, 1983; Mazur & Beauchamp, 2003; Vogel & Beauchamp, 1999). Second, reaction distances of piscivorous fishes are roughly fivefold greater than their prey, possibly because prey are often planktivorous and therefore use acuity-based visual systems for identifying small prey, whereas piscivores use a contrast-based system to target and pursue larger prey (Breck, 1993; de Robertis et al., 2003). Thus, piscivorous fishes have an inherent visual advantage over prey, which is thought to manifest in higher predation rates at crepuscular light levels because prey lose the ability to visually sense predators.

However, in social prey, anti-predator behaviours also involve visually sensing and responding to one another (Herbert-Read et al., 2015; Pertzelan et al., 2023; Ryer & Olla, 1998). For example, when individuals on the edge of a social group initiate a threat response, this can trigger an escape wave throughout the group (Herbert-Read et al., 2015; Pertzelan et al., 2023). Such collective behaviours likely play a key role in reducing prey vulnerability to piscivorous fishes (Lombana & Porfiri, 2022; Pertzelan et al., 2023) but are themselves vulnerable to low-light levels. As visual capability diminishes, the distance between individuals within a social group, or the nearest neighbour distance (NND), increases (Chamberlain & Ioannou, 2019) potentially due to lack of sensory ability or a reduced perceived risk (Azuma & Iwata, 1994; Chamberlain & Ioannou, 2019; Gruber et al., 2019; Pertzelan et al., 2023). As groups lose their cohesion, individuals in them become more vulnerable to predators (Einfalt et al., 2015; Herbert-Read et al., 2015; Pavlov & Kasumyan, 2000; Ryer & Olla, 1998). Thus, higher rates of predation at crepuscular periods might additionally involve the deterioration of prey group behaviours with diminishing light. If this is the case, then predation and predator behaviour should not only change with light, but also with the group behaviour of prey.

Artificial light at night (ALAN) acts by extending crepuscular conditions into the night and can thereby artificially concentrate predators and prey under conditions conducive to piscivorous predation (Gaston et al., 2013; Perkin et al., 2011). For example, in California's Sacramento-San Joaquin Delta, piscivorous fishes including largemouth bass (*Micropterus salmoides*), which is an ambush predator, aggregate around sources of ALAN and predate juvenile salmonids, such as rainbow trout (*Oncorhynchus mykiss*), as they rear and migrate through this freshwater estuary (Nelson et al., 2021, 2022). Here, the presence of ALAN 3–5 h after sunset has been shown to increase the relative predation risk of tethered Chinook salmon (*Oncorhynchus tshawytscha*) smolts roughly sevenfold over the observed lux range of 0–70 lux (Nelson et al., 2021).

The visual systems of largemouth bass and rainbow trout are particularly well-resolved in the context of their respective predator–prey interactions. Available evidence suggests that rainbow trout is most adept at visually sensing and responding to predators under relatively high light levels. While Mazur and Beauchamp (2003) found the reaction distance of rainbow trout peaks at 20.0 lux, it is important to note that the minimum scotopic visual response of rainbow trout to a shadow occurs at 0.01 lux (Rader et al., 2007). By contrast, largemouth bass is a low-light specialist: its reaction distance begins peaking at 1.49 lux and saturates at 5.59 lux (Howick & O'Brien, 1983), and its foraging success peaks under similarly low-light levels (McMahon & Holanov, 1995).

While the current dogma proposes that the visual advantage of piscivorous predators over prey explains the higher rates of piscivorous predation observed in the field under crepuscular light levels, to date no studies have experimentally evaluated the potential role of prey group behaviour in mediating this ecological pattern. For example, in laboratory studies that specifically focus on the impact of light level on largemouth bass piscivorous predation, predators are either subjected to trials with individual prey (e.g. Howick & O'Brien, 1983), or end-of-trial predation rates are reported without any consideration of prey behaviour (e.g. McMahon & Holanov, 1995). Furthermore, no relevant studies that we are aware of have used rainbow trout as prey, despite reaction distance as a function of light level being particularly well-resolved for this species (Mazur & Beauchamp, 2003; Rader et al., 2007).

To address these knowledge gaps, we exposed groups of predator-naïve, hatchery-raised juvenile rainbow trout to natural-origin largemouth bass under three light treatments. The 'high' treatment of 20.0 lux (range 21.4 to 19.7 lux), which represented brighter crepuscular periods or direct, low-intensity ALAN illumination, was that needed for peak reaction distance of trout and above that needed for bass. The 'medium' treatment of 0.50 lux (range 0.53 to 0.49), which mimicked dimmer crepuscular periods or sky glow from distant ALAN, was about one third that needed for peak reaction distances of bass and just above the minimum threshold for vision in trout. The 'low' treatment of 0.005 lux (range 0.006 to 0.005), which was representative of night or no ALAN, was below the threshold for vision in both species.

From video recordings of predation trials, we quantified prey group cohesion in terms of NND and angular deviation (AD), or how close together and similarly oriented prey were, respectively (Azuma & Iwata, 1994; Burford et al., 2022; Chamberlain & Ioannou, 2019). Predator behaviour relevant to their interactions with prey was quantified for each trial using four metrics: (1) predation, or the total number of successful prey captures; (2) attacks, or the total number of events where a predator attempted to capture prey, including both those that did and did not result in predation; (3) attack given interest, or the probability that an interested predator decided to attack; and (4) predation given attack, or the probability that attacks resulted in predation (Einfalt et al., 2015; Gardiner & Motta, 2012; Howick & O'Brien, 1983). We then statistically evaluated potential relationships between light treatment, prey group cohesion and predator behaviour.

We hypothesized that prey would be closer together (smaller NND) and more aligned (smaller AD) under higher light levels. Reduction of NND and AD might also occur as trial time progressed, given that prey would be more likely to encounter or sense the predator and other agitated prey. In addition, we expected that prey group cohesion would change if an observation followed an attack or a predation event, and for the effects of elapsed trial time and previous attacks to vary with light level. While the potential effects of elapsed trial time and previous attacks were not a focus of our study, we included them in our NND and AD analyses to account for any biases they would introduce. Similarly, we accounted for the possibility that some trout groups could be more or less cohesive on average than others.

We hypothesized that predation and attacks would both be highest under the medium light treatment. We also hypothesized that prey group behaviour would influence both predation and attacks, and that this effect could vary by light level. In addition, we expected that the time of day a trial occurred and the duration that a predator was in captivity could influence both responses. While the potential effects of time of day and duration in captivity were not a focus of our study, we included them in our analysis to account for any biases they would introduce. Similarly, we accounted for the possibility that some predators might exhibit more or less predation and attacks than others on average. With regard to attack given interest and predation given attack: Our hypotheses for impact of light level and prey group cohesion, as well as the process by which we accounted for the potential effects of time of day, duration in captivity and predator identity, followed those of predation and attacks.

2 | MATERIALS AND METHODS

2.1 | Fish acquisition and husbandry

All fish were handled in accordance with Animal Care and Use Committee (IACUC) of University of Santa Cruz guidelines (approval no. Danne2207). We acquired rainbow trout from Thomas Fish CO. LLC located in Anderson, California, U.S.A on 9/20/22, 10/20/22, 11/15/22 and 11/30/22. We used fish hatched on multiple dates to allow for similar prey sizes across trials. Trout were weighed in water before the start of each trial; on average mass was 1.80 g, with a range of 1.03 to 2.70 g. Trout fork length was not measured to avoid handling stress.

Twenty largemouth bass were collected in the San Joaquin River outside of Stockton, California, U.S.A. (California scientific collection permit no. S-201120001-20,122-002) using hook and line and transported to our aquarium facility on 9/20/22. Each bass was weighed, measured, injected with a passive integrated transponder (PIT) tag (Biomark) and treated for potential pathogens by placing them in coolers with a 1% salt solution and antibiotics for 8 h. Prior to being injected with the PIT tags, bass were anesthetised in a bath of 90 mgL-1 MS-222 buffered with 360 mgL-1 sodium bicarbonate until they lost equilibrium. After tagging, we monitored the bass until they regained equilibrium and then returned them to their holding tanks. On average, bass mass was 191.4 g, with a range of 109.9 to 303.4 g; on average, bass fork length was 232 mm, with a range of 198 to 272 mm.

All fish were held in the same freshwater aquarium system under flow-through conditions. Bass were kept at 18.0°C in three circular tanks measuring 233 cm in diameter and 135 cm in height (6–7 bass per tank), where they were allowed to swim freely together and fed two trout per bass twice a week. Trout were held in three separate tanks (two circular tanks measuring 91 cm in diameter and 73 cm in height and one flume tank measuring 470 cm × 92 cm × 76 cm) at 15.0°C and fed pellets daily at 4% tank biomass from 12-h belt feeders (FIAP).

2.2 | Experimental design

Experimental trials took place in a circular tank (91.0 cm high, 180 cm diameter; Figure 1). Tank diameter was estimated to be 2.30 largemouth bass reaction distances wide under the high light treatment of 20.0 lux using the peak reaction distances of largemouth bass to 3.7–10 cm bluegill at 5.59 lux according to Howick and O'Brien (1983). The tank was illuminated using an adjustable LED bulb with a natural daylight spectral range (Sanofuturion, WIFIBLE-A19, 6500 Kelvin) mounted above the tank. A perforated cardboard shade was placed over the bulb to dim

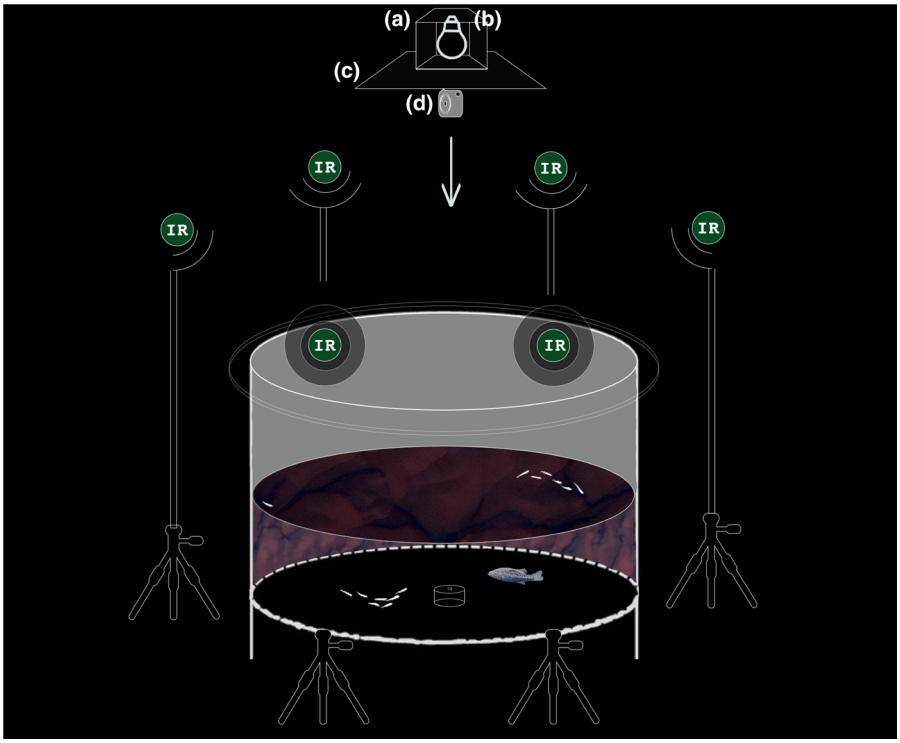

FIGURE 1 Diagram of experimental setup inside tent enclosure. The setup included (a) a cardboard shade to condense and filter light, (b) a programmable LED light, (c) a photo diffuser and (d) a GoPro.

the light during low and medium treatments, and a white silk photo diffuser was placed under the LED bulb to reduce glare and diffuse light evenly in all treatments. Six near-infrared lights (ABI, 850 nm) were spaced evenly above and around the tank. Near-infrared is outside the visible spectrum of fishes (Gardiner & Motta, 2012; Hawryshyn & Harosi, 1994; Mazur & Beauchamp, 2006) but was visible with the near-infrared enabled camera used to record trials (GoPro, Hero 7), which was mounted above the centre of the tank.

The experimental tank was filled to a depth of 48.0 cm (approximately 1230 L), which was the maximum depth that trout were still adequately illuminated by near-infrared lights. This depth was also ~2x the average bass length, in alignment with the depths used in aquarium studies of fishes where subsequent analyses were conducted on two-dimensional positions (e.g. Chamberlain & Ioannou, 2019; Ryer & Olla, 1998). Tank sides were covered with a non-reflective matte black plastic film to reduce glare, and the bottom was covered in white film to enhance the visibility of fish during video analysis. The entire tank setup was surrounded by a tent structure to block any outside stimuli or light. For each trial, light level was recorded using a lux meter at the water surface (International Light Technologies, ILT2400).

The order of the light levels tested was alternated between trial days to minimize any impact of time of day on the dependent variables. Temperature during trials averaged 17.8°C, with a range of 16.9 to 18.5°C. Accordingly, trout groups were temperature adjusted for 20 min prior to the start of trials. To standardize hunger levels, bass were used in one trial per week and fasted for 48 h prior to trial start. Each individual bass was tested an equal number of times at each light level.

Some predation trial protocols acclimate either the predator or the prey to the trial arena before adding the other group of fish (e.g. Einfalt et al., 2015; Howick & O'Brien, 1983). During preliminary trials, we found that researchers entering the tented trial area disturbed fish and resulted in abnormal behaviour. We therefore elected to add both predator and prey simultaneously at the start of a trial and extended the trial time to 1 hour to allow fish to adjust to experimental conditions. Fifteen trout and one bass were used in each trial, at the end of which bass were returned to their holding tank, and all remaining trout were counted and killed according to IACUC guidelines.

2.3 | Video review

We digitally marked the location of all fish in video frames 10, 20, 30, 40 and 50 min from the start of the trial using MATLAB app DLTdv8 (Hedrick, 2008). In each frame, the head and dorsal fin of all trout were digitized, as well as the head of the bass. If any fish were obscured, then the closest frame to the time mark containing all unobscured fish was used instead.

Using Adobe Premiere Pro, the following five events were time-stamped from the video footage of each trial: (1) start of trial, (2) end of trial, (3) interest, (4) attack and (5) predation. 'Interest' occurred when bass repositioned to visually inspect and track a single trout with both eyes (Figure 2, Video S1) and is similar to the terms 'encounter' (Mazur & Beauchamp, 2006), 'reaction' (Howick & O'Brien, 1983; Mazur & Beauchamp, 2003; Vogel & Beauchamp, 1999), and 'detection' (Nyberg, 1971). However, interest did not necessarily precede a capture

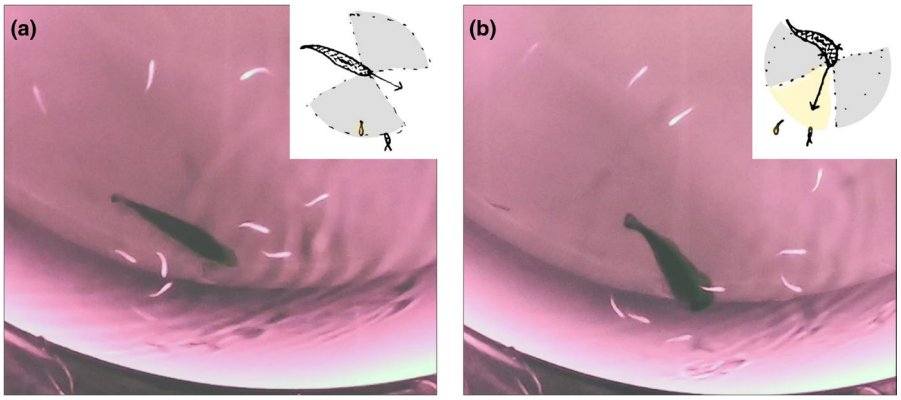

FIGURE 2 A predator demonstrating 'interest'. Interest occurred when bass repositioned to visually inspect and track a single trout (Video S1). Note the change in the bass's heading apparent between panels (a and b), which occurred when it began tracking a single trout.

attempt, as bass could lose interest before attacking. If bass swam by one or more trout without changing heading, we determined there to be no interest. An 'attack' occurred when bass actively attempted to capture a single trout through either ram, chase (Video S2) or suction feeding (Einfalt et al., 2015). An attack began when bass moved toward a trout that it was interested in and ended with the start of jaw depression (Gardiner & Motta, 2012). Attacks typically involved a single burst of swimming of several body lengths and usually concluded with a single visible mouth flare. If a predator sustained speed while targeting a single trout, multiple swallowing attempts were considered a single attack. If jaw movement was unclear, an attack ended when bass predated the targeted trout, stopped chasing it, or became interested in a new trout. 'Predation' occurred when bass had successfully captured trout by completely engulfing the fish in its mouth following an attack (Howick & O'Brien, 1983, Video S3). Occasionally a bass would repeatedly engulf and spit out the same trout for a short period of time (Video S4); this was classified as a single predation event.

2.4 | Statistical analyses

All analyses were conducted in R version 4.1.0 (R Core Team, 2021). Continuous predictors were z-scored (difference between value and mean divided by standard deviation) prior to model fitting given they were often on different scales. Mixed models were fit using the 'lme4' package (Bates et al., 2015), and generalized mixed models were diagnosed using the 'DHARMa' package (Hartig, 2022). Nakagawa's R^2 for mixed models was determined using the 'performance' package (Lüdecke et al., 2021) and is reported alongside degrees of freedom for each model in relevant figure captions.

2.4.1 | Prey group cohesion

We examined two metrics of prey group behaviour that quantified group cohesion: NND and AD, or how close together and similarly oriented prey were, respectively. NND was determined for each trout using a distance matrix (determined using points marked on fish heads) and filtering for the minimum value. AD was determined by calculating the difference between each trout's heading (determined using points marked on fish head and dorsal fin) and the median group heading. NND and AD were calculated from fish positions in five frames from each trial taken at 10-min intervals from elapsed trial time (i.e. 10, 20, 30, 40 and 50 min from the start of the trial). For each analysed frame, the median NND and AD were used in subsequent analyses. Thus, the level of observation was frame, yielding a sample size of $n = 483$ observations distributed among 97 trials (i.e. 97 unique groups of trout).

We assessed how prey group cohesion was related to light level using linear mixed-effects regressions (LMERs) for NND and AD. According to our hypotheses, both models contained fixed effects of light level, elapsed trial time, and a binomial variable indicating whether an observation occurred after an attack. The latter two predictors included interactions with light level. Both models also included a random intercept term for trial (i.e. trout group).

2.4.2 | Predator behaviour

We examined four metrics of predator behaviour that quantified their interactions with prey: (1) predation, or the total number of successful prey captures per trial; (2) attacks, or the total number of events where a predator attempted to capture prey per trial, including both those that did and did not result in predation; (3) attack given interest, or the probability that an interested predator decided to attack; and (4) predation given attack, or the probability that attacks resulted in predation.

Potential relationships between predator behaviour, light level and prey group behaviour were assessed using generalized linear mixed-effects regressions (GLMERs). Given that NND and AD covaried with light level (Figure 3, Table 1), raw metrics could not be used in predator behaviour GLMERs. Instead, prey group NND and AD were, respectively, represented by the NND and AD random intercepts for each trout group from relevant LMERs. This fixed effect therefore represented how prey groups were more or less cohesive than expected, given experimental conditions for each trial.

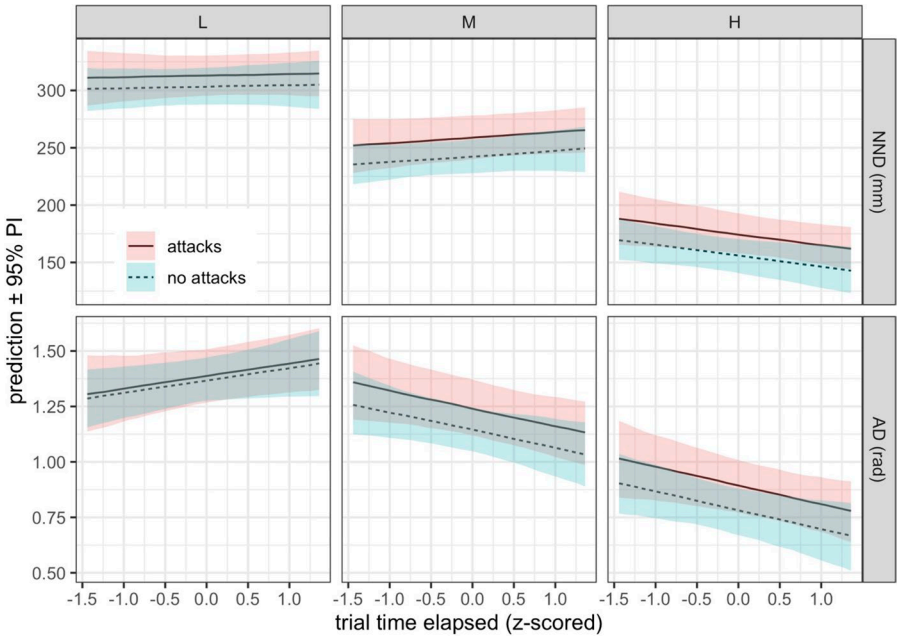

FIGURE 3 Prey were closest together when light level was highest and with no attacks. Lines show predictions of LMERs of NND ($R^2 = 0.59$, residual df = 472) and AD ($R^2 = 0.25$, residual df = 472) and ribbons the respective bootstrapped prediction intervals (PIs), shaded by attack category. L, M and H correspond to low, medium and high light levels, respectively. Higher response values indicate lower group cohesion. Plotted predictions show the interaction between light level and trial time elapsed ($p = 0.03$ for NND and $p = 0.01$ for AD, Table 1). Predictions were made across the full range of trial time elapsed, following and not following attacks, and averaged over the random effect of prey group.

TABLE 1 Analysis of deviance table (Type II Wald *F* tests with Kenward–Roger df) for fixed effects of nearest neighbour distance (NND) and angular deviation (AD) LMERs.

NND	*F*	df	Residual df	*p*
Light	140.64	2	91.32	<0.001
Trial time elapsed	0.10	1	414.31	0.75
Attacks	4.79	1	194.10	0.03
Light: trial time elapsed	2.88	2	414.73	0.06
Light: attacks	0.15	2	193.53	0.86
AD	***F***	**df**	**Residual df**	***p***
Light	49.12	2	91.10	<0.001
Trial time elapsed	2.86	1	409.75	0.09
Attacks	2.69	1	151.19	0.10
Light: trial time elapsed	5.02	2	410.08	0.01
Light: attacks	0.37	2	151.34	0.69

For predation and attacks, the level of observation was trial, yielding a sample size of $n = 97$ split among 20 predators. According to our hypotheses, GLMERs for predation and attacks contained fixed effects of light level and prey group NND and AD. Interactions between light level and prey group NND and AD only improved model parsimony for the attacks GLMER, and therefore were not included in the predation GLMER. Model parsimony did not support the inclusion of time of day nor duration in captivity in either model. Both predation and attacks GLMERs included a random intercept term for predator identity and used a Poisson distribution with a log link function.

For attack given interest, the level of observation was events during which predators at least showed interest in prey. This yielded a sample size of $n = 1814$ split among 19 predators (one predator never showed interest in prey and was therefore excluded from this analysis). According to our hypotheses, the attack given interest GLMER included fixed effects of light level and prey group NND and AD random intercepts. Model parsimony supported interactions between light level and prey group NND and AD; while duration in captivity and time of day did not improve model parsimony, their inclusion did improve model diagnostics. The attack given interest GLMER included a random intercept term for predator identity and used a binomial distribution with a logit link function.

For predation given attack, the level of observation was events where predators attacked prey via a failed predation or predation event, yielding a sample size of $n = 682$ split among 14 predators (6 predators never attacked prey and were therefore excluded from this analysis). According to our hypotheses, the predation given attack GLMER contained fixed effects of light level and prey group NND and AD random intercepts. It also included a random intercept term for predator identity and used a binomial distribution with a logit link function. There was no parsimony benefit of including other terms or interactions.

3 | RESULTS

3.1 | Prey group cohesion

Prey most frequently spent time swimming in unorganized (Video S5) or loosely organized groups. When grouping, trout most frequently formed multiple groups, rather than collecting as one group (Video S6). One or more single individuals could frequently be seen transiting the edge of the tank at the surface or maintaining position just below the surface at the tank edge (Video S7). When swimming in more than one group, groups did not always swim in the same direction around the tank (clockwise or counterclockwise).

Light and attacks had a significant effect on prey NND (Table 1): Trout were closest together when light level was highest and under no attacks (NND LMER: $R^2 = 0.59$, residual df = 472) (Figure 3). Light and the interaction between light and trial time elapsed had a significant effect on prey AD (Table 1): trout were more aligned under medium and high light levels and after more trial time had elapsed under high light levels (AD LMER: $R^2 = 0.25$, residual df = 472, Figure 3).

3.2 | Predator behaviour

Consistent with wild predator behaviours observed by Becker et al. (2013) and Howick and O'Brien (1983), the most commonly observed largemouth bass behaviour was 'slow meandering' (slowly swimming in a non-linear, non-circular fashion about the tank at various depths), while 'rapid swimming' (faster swimming resulting in frequent circuits of the tank space, not including burst or chase activity) was least common. We also observed bass to be differentially active, with some exhibiting continuous movement throughout the experiment, and other fish remaining near the bottom of the tank or circling the drain cap.

Bass exhibited individual variation in attacks and predation (Figure S1): in general, both metrics were positively associated–for example, fish that were above average in terms of number of attacks were also above average in terms of predation. Bass also exhibited individual variation in attack given interest and predation given attack (Figure S1). Interestingly, bass that had the highest probability of predation given attack were those that were relatively average in terms of attacks and predation. Most bass that were well above average in terms of predation were also well above average in terms of the number of attacks and therefore had relatively low probabilities of predation given attack (Figure S1).

Light had a significant effect on attacks, but not on predation (Table 2): attacks were most numerous under high and medium light levels (attack GLMER: $R^2 = 0.92$, residual df = 87) (predation GLMER: $R^2 = 0.73$, residual df = 9, Figure 4). Prey group NND random intercept had a significant effect on both predation and attacks (Table 2): the farther apart trout were relative to expected spacing, the more common both events were (Figure 4). Note that the effect of wider spacing between prey on response variables appeared smallest for attacks under the high light level (Figure 4), but the interaction between light level and NND was not significant in this model (Table 2). Also note that AD had no discernible effect on the frequency of predation, and higher AD (i.e. prey being more dissimilar in orientation) was only associated with an increase in the number of attacks under the low-light treatment (relationship not shown, but see Table 2 for the significance of interaction in the model).

Prey group NND random intercept had a significant effect on attack given interest, but light level did not (Table 3): The farther apart the trout were relative to expected spacing, the more likely that an interested bass attacked (attack given interest GLMER: $R^2 = 0.08$, residual df = 1802, Figure 5). This effect appeared smallest for attack given interest under the high light level (Figure 5), but the interaction between light level and NND was not significant in this model (Table 3). Under the medium light treatment, higher AD was associated with the decreased probability that predators attacked trout they were interested in (relationship not shown, but see Table 3 for significance of interaction in model). That is, prey grouping effectively deterred attacks, even as prey group coordination associated with anti-predator benefits deteriorated.

We found that light had a significant effect on predation given attack (Table 3): Predation was least likely to result from an attack under the high light level (predation given attack GLMER: $R^2 = 0.06$,

TABLE 2 Analysis of deviance table (Type II Wald chi-square tests) for fixed effects of predation and attack GLMERs.

Predation	Chisq	df	p
Light	2.81	2	0.25
Prey group NND random intercept	12.61	1	<0.01
Prey group AD random intercept	0.19	1	0.66
Attacks	**Chisq**	**df**	**p**
Light	26.03	2	<0.01
Prey group NND random intercept	18.46	1	<0.01
Prey group AD random intercept	0.40	1	0.53
Light: prey group NND random intercept	5.20	2	0.07
Light: prey group AD random intercept	7.59	2	0.02

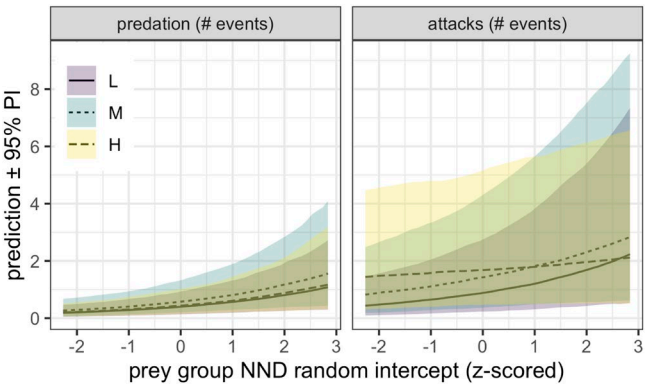

FIGURE 4 Predation and attacks changed more with prey group cohesion than with light level. Lines show predictions of GLMERs of predation ($R^2 = 0.73$, residual df = 9) and attacks ($R^2 = 0.92$, residual df = 87). Ribbons show the respective bootstrapped prediction intervals (PIs) and are shaded by light level. L, M and H correspond to low, medium and high light levels, respectively. Plotted predictions show the interaction between light level and prey group NND random intercept ($p < 0.01$ for predation and for attacks). Predictions shown were made at median AD and averaged over the random effect of individual predator.

TABLE 3 Analysis of deviance table (Type II Wald chi-square tests) for fixed effects of attack given interest and predation efficiency GLMERs.

Attack given interest	Chisq	df	*p*
Light	1.54	2	0.46
Duration in captivity	0.81	1	0.37
Time of day	0.76	1	0.38
Prey group NND random intercept	8.44	1	<0.01
Prey group AD random intercept	0.31	1	0.58
Light: prey group NND random intercept	1.18	2	0.55
Light: prey group AD random intercept	15.47	2	<0.01
Predation given attack	**Chisq**	**df**	***p***
Light	8.77	2	0.01
Prey group NND random intercept	5.23	1	0.02
Prey group AD random intercept	1.12	1	0.29

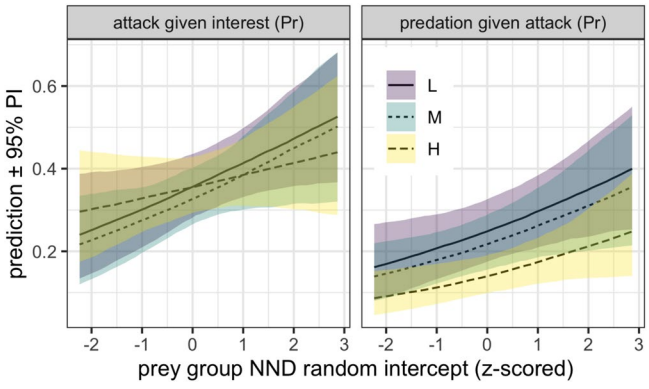

FIGURE 5 Predator attack given interest was influenced most by prey group cohesion, while predation given attack additionally depended on light level. Lines show predictions of GLMERs of attack given interest ($R^2 = 0.08$, residual df = 1802) and predation given attack ($R^2 = 0.06$, residual df = 676). L, M and H correspond to low, medium and high light levels, respectively. Ribbons show the respective bootstrapped prediction intervals (PIs) and are shaded by light level. Plotted predictions show the interaction between light level and prey group NND random intercept ($p < 0.01$ for attack given interest and $p = 0.02$ for predation given attack). Predictions shown were made at median AD and averaged over the random effect of individual predator. For attack given interest, predictions were made at the median duration in captivity and time of day. Pr = probability.

residual df = 676, Figure 5). Prey group NND random intercept also had a significant effect on predation given attack (Table 3): The farther apart the trout were relative to expected spacing, the more likely that an interested bass successfully predated fish that it attacked (Figure 5). AD had no discernible effect on predation given attack.

4 | DISCUSSION

The most striking pattern in our data was that prey group cohesion had the largest impact on all metrics of predator behaviour. Like juvenile coho salmon (*O. kisutch*) (Azuma & Iwata, 1994), we found that rainbow trout group cohesion was closely linked to light level. By accounting for the effects of light level and other experimental conditions, we quantified how trout groups were more or less cohesive than would be expected. The farther apart trout were relative to expected spacing, (1) the higher the probability that interested predators would attack (Figure 6: attack given interest, NND), (2) the higher the probability that such attacks would result in trout being consumed (Figure 6: predation given attack, NND), and ultimately, (3) the more frequently trout were attacked (Figure 6: attacks, NND) and consumed by predators (Figure 6: predation, NND). By contrast, the orientation of trout with respect to one another was not as clearly nor consistently associated with predator behaviour (Figure 6: AD). Taken together, our results suggest that when ambush piscivores like largemouth bass are confronted with grouping prey, they wait to attack when prey groups spread out because this confers the highest probability of capturing individuals. As evidenced by our results and previous work (Azuma & Iwata, 1994; Chamberlain & Ioannou, 2019; Pavlov & Kasumyan, 2000; Lombana & Porfiri, 2022), one scenario where prey group cohesion can deteriorate is under lower light levels, probably because individuals lose visual contact with one another. While predators may be better equipped to sense prey under crepuscular light levels than prey are able to sense predators (Howick & O'Brien, 1983), our data show that prey group behaviour mediated predator–prey interactions under such light levels. Thus, if prey can maintain at least some contact with one another under low-light conditions, some protective benefit may be derived from grouping.

Although we found that predation given attack was highest under the medium light level (Figure 6: predation given attack, light), which was designed to represent relatively dim crepuscular conditions or dimmer sources of ALAN, two of our results stand in contrast to what would be expected based on field-based research: (1) We found no significant effect of light level on the frequency of predation (Figure 6: predation, light), and (2) bass most frequently pursued trout under the highest light level, when they were least likely to successfully capture trout (Figure 6: attacks, light). Beyond the fact that laboratory conditions are not representative of natural conditions (e.g. they artificially confine predators and prey), there are three potential explanations for why our results did not precisely replicate the patterns of predation risk with respect to light level obtained from field-based studies. First, laboratory conditions could have altered the behaviour of wild-origin predators (Wiggins et al., 2018), which were only acclimated for 3 weeks before trials began. For example, some individuals would catch and spit out the same trout repeatedly (up to six times), which has been observed occasionally with live fish prey (Linser et al., 1998), and more commonly with less palatable prey in other laboratory-based research (e.g. up to 24 times before rejecting or accepting tadpole prey; Kruse

Response Variable	Predictor Variable: Light (categorical) Low 0.005 Lux	Medium 0.50 Lux	High 20.0 Lux	Effect size	NND (continuous) Low to High	Effect size	AD (continuous) Low to High	Effect size
NND	−	…	+	0.49	na		na	
AD	−	…	+	0.43	na		na	
Predation *(#)*	n.s.			0.30	− to +	0.83	n.s.	0.23
Attacks *(#)*	−	…	+	0.47	− to +	0.71	n.s. (except low light: − to +)	0.55
Attack given interest *(Pr)*	n.s.			0.07	− to +	0.56	n.s. (except medium light: + to −)	0.51
Predation given attack *(Pr)*	+	…	−	0.43	− to +	0.60	n.s.	0.29

FIGURE 6 A schematic summarizing the findings of this study. For the light predictor variable, +, …, and − symbols denote which light treatment (low, medium or high) that had the highest, middle, or lowest value for each response variable, respectively. For NND and AD predictor variables, which were continuous, − and + symbols, respectively, denote the end of the relationship with the lowest or highest value for a given response variable. Effect sizes are all relative to (divided by) the maximum predicted response variable value. Unless otherwise specified, all other predictor variables were held at mean values (i.e. a *z*-score of 0) when determining effect sizes. For NND and AD response variables, effect sizes were determined under 'no attacks' and light level was held at 'medium' (na = not applicable, n.s. = not significant, alpha = 0.05).

& Stone, 1984, Kruse & Francis, 1977), but not in any field-based research that we are aware of. Second, the methodology of predation trials in the field usually restricts the escape behaviours of prey, preventing them from accessing the protective benefits of social grouping. For example, research using predation event recorders involves restrained and isolated prey affixed to floating platforms (Becker et al., 2013; Linehan et al., 2001; Michel et al., 2020; Nelson et al., 2022). As such, results from these experiments are best interpreted as measures of predator activity rather than successful predation (Burford et al., 2026). Third, related piscivorous predators (Florida largemouth bass, *M. salmoides floridanus*) are usually observed in groups rather than solitary (Annett, 1998). Including multiple predators per trial in future laboratory experiments could therefore be more ecologically meaningful, as interactions between predators may facilitate (Rathbun et al., 1980) or limit (Birch, 1957) successful predation. For example, prey groups in our study were predator-naïve and responded to attacks by becoming less cohesive (Figure 2); whether multiple predators would enhance or further disrupt prey group cohesion, and thereby result in different outcomes than we observed with a single predator per trial, is unclear. Observations of natural predator–prey interactions in the wild across gradients of light intensity, which to our knowledge are unavailable in the literature, would help resolve the discrepancy between our results and those obtained in the field.

In a field study, Nelson et al. (2021) found that early in the night (1–3 h past sunset), predator density and relative predation risk of tethered juvenile Chinook salmon (*O. tshawytscha*) smolts were unrelated to ALAN, but in the following 2 h (3–5 h past sunset), ALAN increased predator density and relative predation risk of tethered smolts. Given that experimental trials in our study occurred for 1 h each during daylight hours, additional aquarium studies could be conducted at night and with longer trial durations to resolve any effects of time of night or long-term ALAN exposure on predatory-prey interactions under laboratory conditions. Another caveat to note is that, in order to avoid disturbing the study subjects and mitigate any effects of differential acclimation durations between predator and prey, we introduced them simultaneously at the beginning of each trial. Therefore, it is possible that handling stress or features of the experimental tank altered behaviour. If future studies decide to use an acclimation period, we advise that they first resolve the necessary acclimation duration for all species tested, as acclimation rates can vary within and among species (Makaras et al., 2021). Nevertheless, we note that some studies evaluating the impact of light level on reaction distances reduced experiment time from 1–4 h to 0.5–1 h because initial video review demonstrated that a sufficient number of predator–prey encounters occurred during the beginning of experiments (Mazur & Beauchamp, 2003; Vogel & Beauchamp, 1999). Finally, we note that our experimental tank was filled to a depth of 48.0 cm, but we did not account for the depth when quantifying fish positions. Similar to our experiment, studies using 2-dimensional tracking or position data have filled tanks to a depth of roughly 2-4x the length of studied fish (e.g. Chamberlain & Ioannou, 2019; Ryer & Olla, 1998). However, future efforts might incorporate multiple camera angles to generate three-dimensional fish position data.

For native fish populations already in decline due to other anthropogenic modifications (e.g. Chinook salmon in California due to an era of hydrologic engineering; Munsch et al., 2022), ALAN reduction could measurably benefit imperilled populations by reducing predation risk and preserving natural light levels that act as migration initiation thresholds (Jägerbrand & Bouroussis, 2021; Tabor et al., 2004). Accordingly, laboratory- or field-based research can point to specific ALAN intensities to be mitigated by relevant management actions. For example, sockeye salmon (*O. nerka*) fry hold position in the presence of light, becoming more exploratory under darkness of <0.1 lux (Tabor et al., 2004). This 0.10 lux threshold suggests that very low levels of ALAN have the potential to modify fry migratory behaviour. At similarly low-light levels (0.005 and 0.50 lux), we found increased probability of predation given attack by bass, which resulted from increased spacing between trout prey (Figure 6). Such low-light levels can be pervasive in urban areas, spreading out widely from ALAN sources, for instance via sky glow. At higher light levels, Mazur and Beauchamp (2006) showed that nocturnal cutthroat trout (*O. clarkii*), aided by urban light pollution, hunted as effectively during illuminated nights (2 lux) as they did under brighter, naturally lit conditions (10.0 lux). While predation may have been minimal under the 20.0 lux treatment in our study, higher frequency of attacks could contribute to a 'landscape of fear', which may have long-term physiological, behavioural, and life-history impacts (Lima & Dill, 1990), which were not measured in our study. Furthermore, while a higher frequency of attacks under bright conditions was not associated with increased predation in our study, this strategy could be more effective in natural settings. For instance, under warm, low-oxygen conditions, which naturally occur in the Sacramento-San Joaquin Delta, the physiological adaptations of largemouth bass allow it to maintain higher levels of aerobic activity than salmonid prey (Burford et al., 2026). Thus, as the prey's ability to recover from bouts of predator escape diminishes, persistent predator attacks may eventually become successful even under bright conditions.

Understanding how environmental conditions govern predator–prey interactions should enhance our ability to predict how key species will respond to changing environmental conditions. At 20.0 lux, we found that bass were least effective at capturing trout, despite exhibiting the most effort (Figure 6). This co-occurred with trout groups being the most cohesive, suggesting a role of collective behaviour in predator evasion. Mechanistically, piscivorous predation is usually explained through visual foraging models in which predators have a physiological advantage during low-light crepuscular hours. In these models, a pelagic predator's ability to successfully encounter, attack and consume prey depends more on the spatial–temporal overlap of suitable environmental conditions (e.g. light, turbidity and temperature), and the size-dependent vulnerability of prey, than on the absolute abundance or density of prey (Mazur & Beauchamp, 2006). As such, these models could miss the potential benefits of prey grouping behaviours, which can include enhanced predator detection, predator confusion and risk dilution (Pertzelan et al., 2023; Treherne & Foster, 1981). Our results suggest that prey risk under laboratory conditions depends more on the cohesion of social groups, and how this changes with light level, than on the light level itself—even for predator behaviour metrics where the effect of light level was significant, the effect size of prey group cohesion was greater than that of light level (Figure 6). Therefore, to more accurately model predation risk in the wild, it might be prudent to incorporate prey group cohesion, and how this depends on light intensity.

AUTHOR CONTRIBUTIONS

Jessica R Frey, Benjamin P. Burford, Rebecca R. Robinson, Lance K. Takata and Brendan M. Lehman conceived the ideas and designed methodology; Jessica R. Frey, Rebecca R. Robinson and Lance K. Takata collected the data; Benjamin P. Burford and Cyril J. Michel analysed the data; Jessica R. Frey and Benjamin P. Burford led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data from the manuscript that have been made publicly available through the Environmental Data Initiative (EDI): https://doi.org/10.6073/pasta/1842da9d50a94af15fe118cdc6d78b99 (Takata, 2025, Accessed 2025-10-17).

ORCID

Jessica R. Frey https://orcid.org/0009-0001-2293-7115
Benjamin P. Burford https://orcid.org/0000-0002-2120-3769
Rebecca R. Robinson https://orcid.org/0000-0001-6866-6907
Lance K. Takata https://orcid.org/0009-0002-7241-1127
Brendan M. Lehman https://orcid.org/0000-0002-6206-6932
Cyril J. Michel https://orcid.org/0000-0002-1198-3837

REFERENCES

Annett, C. A. (1998). Hunting behavior of Florida largemouth bass, *Micropterus salmoides* floridanus, in a channelized river. *Environmental Biology of Fishes*, *53*, 75–87. https://doi.org/10.1023/A:1007419902535

Azuma, T., & Iwata, M. (1994). Influences of illumination intensity on the nearest neighbour distance in coho salmon Oncorhynchus kisutch. *Journal of Fish Biology*, *45*(6), 1113–1118. https://doi.org/10.1111/j.1095-8649.1994.tb01077.x

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Becker, A., Whitfield, A. K., Cowley, P. D., Järnegren, J., & Næsje, T. F. (2013). Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *Journal of Applied Ecology*, *50*(1), 43–50. https://doi.org/10.1111/1365-2664.12024

Birch, L. C. (1957). The meanings of competition. *The American Naturalist*, *91*(856), 5–18. https://doi.org/10.1086/281957

Breck, J. E. (1993). Foraging theory and piscivorous fish: Are forage fish just big zooplankton? *Transactions of the American Fisheries Society*, *122*, 902–911. https://doi.org/10.1577/1548-8659(1993)122<0902:FTAPFA>2.3.CO;2

Burford, B. P., Lehman, B. M., Zillig, K. W., Lo, V. K., McInturf, A. G., Kwan, G. T., Cocherell, D. E., Fangue, N. A., & Michel, C. J. (2026). Linking

aerobic scope to fitness in the wild reveals potential opportunities to help recover imperiled salmon populations. *Communications Biology*, *9*, 359. https://doi.org/10.1038/s42003-026-09642-7

Burford, B. P., Williams, R. R., Demetras, N. J., Carey, N., Goldbogen, J., Gilly, W. F., Harding, J., & Denny, M. W. (2022). The limits of convergence in the collective behavior of competing marine taxa. *Ecology and Evolution*, *12*(3), e8747. https://doi.org/10.1002/ece3.8747

Cerri, R. D. (1983). The effect of light intensity on predator and prey behaviour in cyprinid fish: Factors that influence prey risk. *Animal Behaviour*, *31*, 736–742. https://doi.org/10.1016/S0003-3472(83)80230-9

Chamberlain, A. C., & Ioannou, C. C. (2019). Turbidity increases risk perception but constrains collective behaviour during foraging by fish shoals. *Animal Behaviour*, *156*, 129–138. https://doi.org/10.1016/j.anbehav.2019.08.012

de Robertis, A., Ryer, C. H., Veloza, A., & Brodeur, R. D. (2003). Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. *Canadian Journal of Fisheries and Aquatic Sciences*, *60*(12), 1517–1526. https://doi.org/10.1139/f03-123

Einfalt, L. M., Parkos, J. J., & Wahl, D. H. (2015). Effect of predator size and prey characteristics on Piscivory of juvenile largemouth bass. *Transactions of the American Fisheries Society*, *144*(4), 682–692. https://doi.org/10.1080/00028487.2015.1027002

Gardiner, J. M., & Motta, P. J. (2012). Largemouth bass (*Micropterus salmoides*) switch feeding modalities in response to sensory deprivation. *Zoology*, *115*(2), 78–83. https://doi.org/10.1016/j.zool.2011.09.004

Gaston, K. J., Bennie, J., Davies, T. W., & Hopkins, J. (2013). The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biological Reviews*, *88*(4), 912–927. https://doi.org/10.1111/brv.12036

Gruber, D. F., Phillips, B. T., O'Brien, R., Boominathan, V., Veeraraghavan, A., & Vasan, G. (2019). Bioluminescent flashes drive nighttime schooling behavior and synchronized swimming dynamics in flashlight fish. *PLoS One*, *14*(8), e0219852. https://doi.org/10.1371/journal.pone.0219852

Hartig, F. (2022). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hawryshyn, C. W., & Harosi, F. I. (1994). Spectral characteristics of visual pigments in rainbow trout (Oncorhynchus). *Vision Research*, *34*(11), 1385–1392. https://doi.org/10.1016/0042-6989(94)90137-6

Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspiration & Biomimetics*, *3*(3), 034001. https://doi.org/10.1088/1748-3182/3/3/034001

Herbert-Read, J. E., Buhl, J., Hu, F., Ward, A. J. W., & Sumpter, D. J. T. (2015). Initiation and spread of escape waves within animal groups. *Royal Society Open Science*, *2*(4), 140355. https://doi.org/10.1098/rsos.140355

Howick, G. L., & O'Brien, W. J. (1983). Piscivorous feeding behavior of largemouth bass: An experimental analysis. *Transactions of the American Fisheries Society*, *112*(4), 508–516. https://doi.org/10.1577/1548-8659(1983)112<508:pfbolb>2.0.co;2

Jägerbrand, A. K., & Bouroussis, C. A. (2021). Ecological impact of artificial light at night: Effective strategies and measures to deal with protected species and habitats. *Sustainability*, *13*(11), 5991. https://doi.org/10.3390/su13115991

Kruse, K. C., & Francis, M. G. (1977). A predation deterrent in larvae of the bullfrog, *Rana catesbeiana*. *Transactions of the American Fisheries Society*, *106*(3), 248–252. https://doi.org/10.1577/1548-8659(1977)106<248:apdilo>2.0.co;2

Kruse, K. C., & Stone, B. M. (1984). Laregmouth bass (*Micropterus salmoides*) learn to avoid feeding on toad (Bufo) tadpoles. *Animal Behaviour*, *32*(4), 1035–1039. https://doi.org/10.1016/S0003-3472(84)80218-3

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Linehan, J. E., Gregory, R. S., & Schneider, D. C. (2001). Predation risk of age-0 cod Gadus relative to depth and substrate in coastal waters. *Journal of Experimental Marine Biology and Ecology*, *263*(1), 25–44. https://doi.org/10.1016/S0022-0981(01)00287-8

Linser, P. J., Carr, W. E. S., Cate, H. S., Derby, C. D., & Netherton, J. C. (1998). Functional significance of the co-localization of taste buds and teeth in the pharyngeal jaws of the largemouth bass, *Micropterus salmoides*. *Biological Bulletin*, *195*(3), 273–281. https://doi.org/10.2307/1543139

Lombana, D. A. B., & Porfiri, M. (2022). Collective response of fish to combined manipulations of illumination and flow. *Behavioural Processes*, *203*, 104767. https://doi.org/10.1016/j.beproc.2022.104767

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *The Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Makaras, T., Stankevičiūtė, M., Šidagytė-Copilas, E., Virbickas, T., & Razumienė, J. (2021). Acclimation effect on fish behavioural characteristics: Determination of appropriate acclimation period for different species. *Journal of Fish Biology*, *99*(2), 502–512. https://doi.org/10.1111/jfb.14740

Mazur, M. M., & Beauchamp, D. A. (2003). A comparison of visual prey detection among species of piscivorous salmonids: Effects of light and low turbidities. *Environmental Biology of Fishes*, *67*(4), 397–405. https://doi.org/10.1023/A:1025807711512

Mazur, M. M., & Beauchamp, D. A. (2006). Linking piscivory to spatial-temporal distributions of pelagic prey fishes with a visual foraging model. *Journal of Fish Biology*, *69*(1), 151–175. https://doi.org/10.1111/j.1095-8649.2006.01075.x

McMahon, T. E., & Holanov, S. H. (1995). Foraging success of largemouth bass at different light intensities: Implications for time and depth of feeding. *Journal of Fish Biology*, *46*, 759–767. https://doi.org/10.1111/j.1095-8649.1995.tb01599.x

Michel, C. J., Henderson, M. J., Loomis, C. M., Smith, J. M., Demetras, N. J., Iglesias, I. S., Lehman, B. M., & Huff, D. D. (2020). Fish predation on a landscape scale. *Ecosphere*, *11*(6), e03168. https://doi.org/10.1002/ecs2.3168

Munsch, S. H., Greene, C. M., Mantua, N. J., & Satterthwaite, W. H. (2022). One hundred-seventy years of stressors erode salmon fishery climate resilience in California's warming landscape. *Global Change Biology*, *28*(7), 2183–2201. https://doi.org/10.1111/gcb.16029

Nelson, T. R., Michel, C. J., Gary, M. P., Lehman, B. M., Demetras, N. J., Dudley, P. N., Hammen, J. J., & Horn, M. J. (2022). Riverine fish density, predator–prey interactions, and their relationships with artificial light at night. *Ecosphere*, *13*(10), e4261. https://doi.org/10.1002/ecs2.4261

Nelson, T. R., Michel, C. J., Gary, M. P., Lehman, B. M., Demetras, N. J., Hammen, J. J., & Horn, M. J. (2021). Effects of artificial lighting at night on predator density and salmonid predation. *Transactions of the American Fisheries Society*, *150*(2), 147–159. https://doi.org/10.1002/tafs.10286

Nyberg, D. W. (1971). Prey capture in the largemouth bass. *American Midland Naturalist*, *86*(1), 128–144. https://doi.org/10.2307/2423693

Olmsted, L. L. (1974). *The ecology of largemouth bass (Micropterus salmoides) and spotted bass (Micropterus punctulatus) in Lake Fort Smith, Arkansas*. Doctoral dissertation. University of Arkansas.

Pavlov, D. S., & Kasumyan, A. O. (2000). Patterns and mechanisms of schooling behavior in fish: A review. *Journal of Ichthyology*, *40*(2), 163–231. https://www.researchgate.net/publication/264977013

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., & Tockner, K. (2011). The influence of artificial light on stream and riparian ecosystems: Questions, challenges, and perspectives. *Ecosphere*, *2*(11), 122. https://doi.org/10.1890/ES11-00241.1

Pertzelan, A., Ariel, G., & Kiflawi, M. (2023). Schooling of light reflecting fish. *PLoS One*, *18*, e0289026. https://doi.org/10.1371/journal.pone.0289026

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rader, R. B., Belish, T., Young, M. K., & Rothlisberger, J. (2007). The scotopic visual sensitivity of four species of trout: A comparative study. *Western North American Naturalist*, *67*(4), 524–537. https://doi.org/10.3398/1527-0904(2007)67[524:TSVSOF]2.0.CO;2

Rathbun, A. P., Wells, M. C., & Bekoff, M. (1980). Cooperative predation by coyotes on badgers. *Journal of Mammalogy*, *61*(2), 375–376. https://doi.org/10.2307/1380074

Ryer, C. H., & Olla, B. L. (1998). Effect of light on juvenile walleye pollock shoaling and their interaction with predators. *Marine Ecology Progress Series*, *167*, 215–226. https://doi.org/10.3354/meps167215

Tabor, R. A., Brown, G. S., & Luiting, V. T. (2004). The effect of light intensity on sockeye Salmon fry migratory behavior and predation by Cottids in the Cedar River, Washington. *North American Journal of Fisheries Management*, *24*(1), 128–145. https://doi.org/10.1577/m02-095

Takata, L. (2025). *California's Central Valley project improvement act predation contact point study—2022: Predator-prey interactions under low artificial lighting in a laboratory setting ver 1*. Environmental Data Initiative. https://doi.org/10.6073/pasta/1842da9d50a94af15fe118cdc6d78b99

Treherne, J. E., & Foster, W. A. (1981). Group transmission of predator avoidance behaviour in a marine insect: The Trafalgar effect. *Animal Behaviour*, *29*, 911–917. https://doi.org/10.1016/S0003-3472(81)80028-0

Vogel, J. L., & Beauchamp, D. A. (1999). Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(7), 1293–1297. https://doi.org/10.1139/f99-071

Wiggins, W. D., Bounds, S., & Wilder, S. M. (2018). Laboratory-reared and field-collected predators respond differently to same experimental treatments. *Behavioral Ecology and Sociobiology*, *72*(2), 19. https://doi.org/10.1007/s00265-017-2437-7

SUPPORTING INFORMATION

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

Video S1. Bass investigates trout. The reorientation toward individual fish, in this case above the bass in the water column (0:05) constitutes 'interest', the first step toward trout predation.

Video S2. Bass misses a trout.

Video S3. Trout eaten by bass at 0:04 in an example of successful predation.

Video S4. Trout captured by bass at 0:06 is spit out at 0:09, recaptured at 0:15 and spit out again at 0:22. This was classified as one predation event.

Video S5. Trout most frequently swam independently about the tank.

Video S6. Two shoals display different behaviour. One transits the tank frequently changing direction, and one circles the edge of the tank. Trout did not come together as one school under any lighting treatments.

Video S7. One or more single individuals could frequently be seen transiting the edge of the tank at the high water line or maintaining position just below the water's surface at the tank edge. When fish made a fast break, they also tended to follow the water surface rather than dive.

Table S1. The number of replicates and the relevant scale of inference for this study.

Figure S1. Predator identity (ID) random intercepts from predation, attack, attack given interest, and predation given attack GLMERS.

How to cite this article: Frey, J. R., Burford, B. P., Robinson, R. R., Takata, L. K., Lehman, B. M., & Michel, C. J. (2026). Prey group cohesion mediates the outcome of predator–prey interactions under artificial lighting. *Functional Ecology*, *00*, 1–12. https://doi.org/10.1111/1365-2435.70389