



# The role of social network behavior, swimming performance, and fish size in the determination of angling vulnerability in bluegill

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## Abstract

An individual's behavioral and physiological characteristics can have important impacts on fitness, including during interactions with humans. For example, certain traits (metabolic rate, boldness, etc.) have been shown to impact angling vulnerability in fish targeted by recreational anglers. While prior work has focused on boldness behavior and several metrics of metabolic performance, the role of two critical traits, social behavior and swimming performance, have rarely been directly examined. To address this gap, we conducted a study utilizing bluegill *Lepomis macrochirus*, a highly popular sportfish species found throughout much of North America, to determine the relationship between social behavior, swimming performance, fish size, and angling vulnerability. One hundred and seven bluegill were assessed for social behavior in a laboratory setting, using scoring methods derived from social network analysis. Bluegill were then assessed for swimming performance (critical swimming speed,  $U_{crit}$ ) before being angled in a naturalistic pond setting over nine daily angling sessions. Following angling, a subset of fish were left uncaptured ( $N = 28$ ), were captured only once ( $N = 68$ ), or were captured twice ( $N = 11$ ). Both fish total length and swimming performance were positively linked with vulnerability to initial capture, with fish length also being linked to vulnerability to recapture. In addition to length, social behavior (higher sociability and lower aggression) was positively linked to vulnerability to recapture. Collectively, these results indicate that the drivers of angling vulnerability shift as angled fish populations gain more experience with lures, and that for bluegill, the most vulnerable individuals are likely to be larger and highly social.

## Significance statement

Individuals within a species show several differences in their behavior and physiology. These differences may have major consequences for fitness, especially in environments impacted by humans. One example of this is freshwater fish targeted by recreational anglers, where individuals with certain behavioral or physiological traits might be more likely to be caught. In this study, we assessed the social behavior, aggression, and swimming performance of bluegill *Lepomis macrochirus* before angling them in a naturalistic pond setting. We found that larger size and higher swimming performance were linked to vulnerability to initial capture, while length and higher sociability caused fish to be more vulnerable to being caught a second time. Collectively, this means these traits may evolve as a result of selective harvest and also that the drivers of vulnerability may change after fish gain experience with anglers.

**Keywords** Social network analysis · Behavioral syndromes ·  $U_{crit}$  · Fisheries-induced evolution · Sociability

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## Introduction

Within populations, individuals often show consistent differences in behavioral characteristics. These sets of behavioral traits, often referred to as “behavioral syndromes” (Sih et al. 2004; Sih and Bell 2008; Wilson and Godin 2009), include several primary axes, including boldness, exploratory tendency, activity, aggression, and sociability (Réale et al. 2007; Conrad et al. 2011). For species that live in groups, the aggression and sociability axes play a major part in defining the

role of an individual within the group. For instance, highly aggressive individuals may be likely to assume dominant positions within social groups (Winberg et al. 1991; Dugatkin and Wilson 1992), while less aggressive individuals may be forced into subordinate roles where access to resources may be limited (Øverli et al. 1999; Webster et al. 2009). Despite their subordinate position, less-aggressive individuals may benefit by avoiding energetically costly confrontations with other individuals (Houston and McNamara 1988; Seebacher et al. 2013) or by more easily associating with other individuals and gaining the advantages of group membership (Croft et al. 2003; Öst et al. 2015). The relative advantage of any of these social approaches is expected to vary depending on environmental context, including abiotic conditions, population density, predator abundance, and food availability (Dingemanse and Wolf 2010; Sih et al. 2015).

In many cases, interindividual differences in behavior are associated with interindividual differences in physiology as well (Koolhaas et al. 1999). These correlations are often due to tradeoffs between physiology and fitness; for instance, individuals with high metabolic rates tend to be bolder while foraging because they consume energy more quickly and, thus, must forage more actively in order to acquire the food to fuel those metabolic needs (Stamps 2007). Indeed, boldness has often been found to be positively linked with metabolic rate (Careau et al. 2008; Killen et al. 2012; Binder et al. 2016) as well as low glucocorticoid responsiveness to stress (Koolhaas et al. 1999; Archard et al. 2012). In addition to boldness, metabolic characteristics such as aerobic scope and standard metabolic rate have also been positively correlated to aggression and dominance (Metcalf et al. 1995; Killen et al. 2014). For fish, this correlation may be due to the greater swimming performance of fish with higher metabolic rates, which leads to these individuals taking leadership positions within shoals or schools that are preserved through aggressive behavior (Killen et al. 2017; Seebacher and Krause 2017). As a result, a selective pressure that targets a particular physiological trait (such as swimming performance) would also impact the behavioral traits correlated with it, and vice versa (Dochtermann and Roff 2010; Wolf and Weissing 2012).

One circumstance in which individual survival and fitness are linked with behavior and physiology can be found in fish that are targeted by recreational or commercial fishing. It is well documented that behavioral and physiological traits (such as boldness or metabolism) can be drivers of vulnerability to capture (Cooke et al. 2007; Redpath et al. 2010; Lennox et al. 2017), leading to the evolution of those characteristics as a result of selective harvest (Uusi-Heikkilä et al. 2008; Díaz Pauli and Sih 2017); however, the results of studies have been inconsistent. While boldness has been found to be linked to angling vulnerability in common carp *Cyprinus carpio* (Klefoth et al. 2013, 2017) and higher metabolic rates

have been found in largemouth bass *Micropterus salmoides* selected for high vulnerability to angling (Cooke et al. 2007; Redpath et al. 2010), boldness has not been found to be a driver of capture vulnerability in Eurasian perch *Perca fluviatilis* (Vainikka et al. 2016) and has been negatively linked to angling vulnerability in bluegill *Lepomis macrochirus* (Wilson et al. 2011). Furthermore, an artificial selection experiment on zebrafish *Danio rerio* found that even after simulated size-selective harvest, metabolic rate remained unchanged (Uusi-Heikkilä et al. 2015).

While boldness and metabolic rate have been extensively studied in the context of angling vulnerability (Cooke et al. 2007; Klefoth et al. 2013, 2017; Hessenauer et al. 2015), the influence of social behavior on vulnerability is only now being examined. In one example, research on blacktip reef sharks *Carcharhinus melanopterus* found that social networks of sharks were robust to fisheries capture (Mourier et al. 2017), while research using artificially selected lines of zebrafish found that the line of fish subjected to negative size selection (fish over a certain size were safe from angling) experienced a drop in mean sociability as defined by a propensity to shoal with other individuals on the other side of a clear divider (Sbragaglia et al. 2019). Perhaps the most direct study of sociability and its link to angling vulnerability was a study of bluegill by Louison et al. (2018a). In this study, sociability was defined once again as the propensity of an individual to attempt to shoal with a group of conspecifics on the other side of a clear divider, while aggression was assessed in paired dyadic trials. This study found that more social bluegill were more likely to be captured, at least with the angling method used (stationary, artificial bait). However, social behavior in this study was examined in an individual context, where the social behavior of individuals was not impacted by a group of individuals around them. As bluegill are a socially gregarious species that tends to associate in large groups (McCartt et al. 1997), an assessment of social behavior (including willingness to associate with conspecifics as well as aggression) in a group setting will likely be a more robust and ecologically relevant definition of this behavior and its subsequent link to angling vulnerability. Indeed, prior work has shown that individual fish will show different levels of behavior (i.e., altered exploratory tendency or boldness) when tested alone compared to when tested in a group (Jolles et al. 2017) and that the actual composition of behavioral types within a group can have a major impact on behavior (Magnhagen 2012).

In addition to social behavior, little work has been done examining whether performance-based metrics, such as swimming performance, may be linked to angling vulnerability. Indeed, the potential for angling to selectively capture individuals based on their swimming performance has never been assessed (though selection based on swimming activity has, see Binder et al. 2012; Koeck et al. 2018), even though fisheries-induced evolutionary changes in swimming

performance could have major impacts on population fitness (Beecham et al. 2007; Mee et al. 2011). With regard to angling vulnerability, swimming performance could be linked through multiple mechanisms. First, individuals with greater swimming performance could be better able to chase down actively retrieved/trolled lures. Even in the case of a stationary lure or bait (such as is often used for small gamefish such as bluegill) when fish densities are high and competition for the opportunity to feed on the bait is present (Stoner and Ottmar 2004; Ward et al. 2006), individuals with greater performance may be the first to be captured as they are quickest to reach the lure. Second, swimming performance may be a proxy for metabolic rate (Reidy et al. 2000), a characteristic that has been shown to be under angling selection in some previous work (Redpath et al. 2010; Hessenauer et al. 2015). In the specific case of bluegill, while previous work did not show a difference in standard metabolic rate or aerobic scope between captured and uncaptured fish, a relationship was found whereby fish with a shorter recovery time following exhaustive exercise were among the first fish to be captured (Louison et al. 2018b). As recovery time following exercise has been linked with quick response performance in fish (Killen et al. 2015), which in turn could be linked to the speed at which a fish responds to a lure or bait (either to strike or to dart away and avoid), this therefore leaves open the possibility that swimming performance could be linked with angling vulnerability in this species, even though no links have been found between other measures of metabolic phenotype and vulnerability previously.

To define links between angling vulnerability, swimming performance, and social behavior, we conducted a study in bluegill. This species was chosen because it is among the most popular targets for recreational anglers in North America (Gaeta et al. 2013) is a relatively social species that tends to congregate in groups (McCartt et al. 1997), its relatively small size lends itself well to laboratory studies of behavior and physiology, and our previous work on this species (Louison et al. 2018a) allows us to make meaningful comparisons between how behavior in a group setting might impact angling vulnerability, as compared to behavior in an individual setting as was done in that study. To evaluate these behavioral traits in bluegill, groups of focal individuals were loaded together into a behavioral arena, and their sociability and aggression were subsequently evaluated within the framework of social network analysis (Krause et al. 2003; Croft et al. 2005; Wilson et al. 2014). Fish were also assessed for individual swimming performance in a Brett-style swim tunnel (Brett 1964) before being angled in a naturalistic pond setting. We predicted that social behavior (specifically, higher sociability) in a group setting would be positively linked to angling vulnerability, that fish with higher swimming performance would prove to be more vulnerable to angling,

and that social behavior would in turn be positively linked to swimming performance.

## Methods

### Study animals and holding

On 30 March 2017, 365 adult bluegill were captured via hoop netting from Spring Lake, IL, USA, by personnel from Jake Wolf Fish Hatchery in Topeka, IL, USA. Spring Lake is a small (822 ha) lake containing numerous predatory fish species, including largemouth bass *Micropterus salmoides* and muskellunge *Esox masquinoy*. While recreational angling is allowed on Spring Lake, we were informed by hatchery personnel that the bluegill were sampled from a macrophyte-covered area of the lake where angling seldom occurs and that no angling to their knowledge had taken place in the calendar year in that location prior to sampling. Prior research has shown that fish tend to lose learned lure or bait avoidance if angling pressure ceases over a period of a few months or even less (Wegener et al. 2018; Koeck et al. 2019), meaning that it is unlikely that the bluegill used for this study were influenced by prior bait experience even if they had experienced lures in prior years. Following collection, the bluegill were then held in hatchery raceways for 1 week before subsequently being delivered to the Illinois Natural History Survey's Aquatic Research Facility in Champaign, IL, USA, on 5 April 2017. The facility consists of a wet laboratory, outdoor fish-holding tanks, and a series of 24 earthen bottom ponds ranging in total area from 0.04 to 0.12 ha. Of the 365 bluegill originally delivered, the 164 largest adults (total length range = 14.3–19.3 cm, mean total length  $\pm$  standard error of the mean, SEM =  $16.6 \pm 0.1$  cm; body mass range 57.5–152.6 g, mean body mass  $\pm$  SEM =  $93.3 \pm 1.7$  g) were selected for use in this study, with the remaining 201 smaller bluegill stocked into an on-site pond for use in a separate study. Upon selection, adult bluegill were implanted with a 0.8-cm Passive Integrated Transponder tag (PIT, Biomark®, Boise, ID) for individual identification and stocked into one of ten circular 1135 L plastic, holding tanks at a density of 15–17 bluegill per tank. Each holding tank was part of a flow-through system that continuously drew freshwater from an adjacent pond at a rate of  $\sim 8$  full water exchanges per day, and water passively drained back to the pond. Every day during holding, fish were fed frozen bloodworms (Chironomidae) acquired from a local pet store, rationed to provide  $\sim 5\%$  of the average fish's body mass per day.

### Social behavior assay

Assessment of social behavior took place approximately 4 weeks after bluegill arrived at the facility, starting 1

May 2017 and continuing through 21 May 2017. A total of 120 fish were assessed for social behavior. This assessment took place in one of five 565 L rectangular polyethylene stock tanks (hereafter “arenas,” 181 cm long × 65 cm wide) filled with pond water to a depth of 25 cm. Water temperatures in the arenas were maintained near 18 °C for the duration of the experiment, with dissolved oxygen saturation maintained above 90% using a Pentair Sweetwater™ air compressor connected via tubing to an immersed air stone. A total of four sets of behavioral assays were conducted, with five groups of six fish (hereafter referred to as “shoals”) assayed within each set.

On the day before the first set of behavioral assessments, 30 fish were collected from the outdoor holding tanks and tagged for on-camera identification with two circular plastic buttons (1.4 cm diameter, 0.1 cm thickness) in one of six colors (black, green, red, orange, yellow, or white), attached to dorsal spines using 22 gauge art wire in a fashion similar to Wilson et al. (2014). The buttons allowed for the differentiation of individuals during subsequent behavioral scoring, and pilot trials conducted prior to experimentation demonstrated that the tags had minimal impact on swimming behavior. While we were cognizant of the fact that the tag color could potentially impact our findings (Catalano et al. 2001), subsequent analysis showed no difference between tag colors in the net number of aggressive acts (acts given minus acts received, ANOVA,  $F_{5, 114} = 2.23$ ,  $p = 0.055$ ; see definition of aggressive acts below). Following tagging, fish were loaded into behavioral arenas at a density of six fish per arena, with each fish within a shoal having different colored buttons. Fish within each shoal were taken from separate holding tanks to prevent fish interactions from being impacted by familiarity (Keller et al. 2017; Trapp and Bell 2017). In addition, bluegill within each shoal were size matched such that the largest fish in each shoal was no more than 1 cm greater in total length than the smallest fish (approximately 7% difference in size, depending on the mean size of fish in the shoal); previous research on the congeneric pumpkinseed *Lepomis gibbosus* demonstrated that differences in size of this degree are unlikely to impact the direction of aggressive interactions among fish (Beacham 1988). After tagging, bluegill were allowed to acclimate overnight in the arena before the first social behavior observation took place the following morning (Jacoby et al. 2014).

Evaluation of social behavior consisted of once-daily observations over the course of three consecutive days conducted between 8:30 and 11:30 a.m., beginning the day after fish were loaded into the arenas. Immediately prior to the outset of observations, two GoPro™ Hero 3 cameras were mounted over the arenas, and the air stone in the tank was removed to prevent bubbles from shielding fish from the view of the cameras. When videos were later scored for behavior, the first 30 min was discarded as an acclimation period, with behaviors scored during the following 30 min. A 30-min trial period has been shown previously to be of sufficient duration to quantify

social behavior (Morrell et al. 2008; Dyer et al. 2009). At the conclusion of the 30-min observation period on the first and second day, cameras were removed, the air stone was replaced, and fish were fed with bloodworms corresponding to ~5% body weight per fish. Following the third day of observations, bluegill were quickly netted from the arena, had their dorsal fin tags carefully removed, and were placed into one of two 1135 L indoor holding tanks featuring identical water conditions to the behavioral arenas prior to assessment of swimming performance (see below), at a density of 15 fish per tank. This was done to facilitate swimming performance assessment in even blocks over 2 days. If we had left the fish in their original tanks, there would have been an overnight period for the second set of 15 fish where they were kept at a different density than the overnight period for the first set of fish (i.e., if we had assessed fish directly from their social tanks, given that there were six fish in five tanks, there was no way to avoid leaving at least one tank with fewer than six fish overnight). This entire process was repeated for three additional sets, until a total of 20 shoals (120 bluegill) were assayed for social behavior.

### Scoring and extraction of individual social network metrics

Scoring of behavioral trials took place after the conclusion of all aspects of the experiment and was performed by the lead author to ensure consistency. To minimize observer bias, the scorer (lead author MJL) was blinded to each fish’s swimming performance or their angling outcome during scoring. Scoring consisted of the construction of both associative and aggression interaction matrices to quantify social behavior in each shoal, following previously established methods (Cañon Jones et al. 2011), and allowed us to quantify the behavior of individual fish along an axis of sociability–aggression. To compile association data, the location of each fish within the behavioral arena was noted at 1-min intervals within the 30-min observation, for a total of 30 observation points. If the end of the snout of one fish was within one body length of another fish, the two fish were considered to be interacting with each other (Keller et al. 2017). The standard of one body length was determined a priori based on observations from a series of pilot trials, where roughly one body length was a radius where fish either engaged in aggression or continued to remain in proximity until disturbed by other fish. In the event of an interaction pattern featuring more than two fish (i.e., fish A associating with fish B, which was associating with fish C), all individuals were considered to be associating with each other for the purpose of scoring (Croft et al. 2011; Williams et al. 2017). A total of 90 observations were scored over the 3 days of trials for each shoal. Because raw values for social behavior (number of interactions, normalized by the number of interactions across all fish on that day of observation) proved to be

repeatable across the 3 days of testing (intraclass correlation coefficient based on one-way ANOVA = 0.41, 95% confidence interval = 0.30–0.52), we pooled the data from all interactions across all three observation days in constructing the final associative matrix (Büttner et al. 2015).

For the construction of aggression matrices to define dominant and submissive fish within each shoal, each aggressive act (bites, charges, chases) observed throughout the entire 30-min observation period (not only at observation points) that forced the recipient fish to displace itself by at least one body length was tallied and the initiator and recipient of each act was recorded (Cañon Jones et al. 2011). Following scoring of the 3 days of trials aggression matrices, including the compiled number of aggressive acts from each fish toward each of the other five fish, were constructed for each shoal. The data was pooled across all 3 days because, once again, the normalized number of aggressive acts initiated (ICC = 0.35, 95% confidence interval = 0.23–0.46) and the normalized number of acts received (ICC = 0.40, 95% confidence interval = 0.29–0.51) proved to be sufficiently repeatable.

Analysis of all associative and aggression matrices was conducted using UCInet software, version 6.646 (Borgatti et al. 2002). An associative matrix for each shoal was weighted by the number of observation points in which each pair of individuals was found to be associating (Silk et al. 2015). These matrices were used to determine each fish's "weighted degree" within a shoal, a measure of the overall sociability of each fish (Sih et al. 2009; Cañon Jones et al. 2011). For this metric, fish with a higher weighted degree had more total associations with a larger number of shoal mates and were considered to be more social individuals, relative to individuals with a lower weighted degree. Aggression matrices, on the other hand, were directional, taking into account the initiator and recipient of each aggressive act. These matrices were used to compute "indegree centrality" and "outdegree centrality" for each fish. Briefly, outdegree centrality is a measure of aggression, whereby individuals with high outdegree centrality directed a large number of aggressive attacks toward shoalmates. Inversely, high values of indegree centrality indicate being frequently attacked by shoalmates (Cañon Jones et al. 2010). Because measures of social behavior for each individual are not independent and are impacted by the social behavior of the surrounding individuals in that shoal (Croft et al. 2011; Magnhagen 2012), we divided weighted degree, indegree centrality, and outdegree centrality by the average values for each shoal, in order to control for shoal effects on behavior. Following conclusion of the trials and extraction of social network metrics, we found no effect of the amount of set on weighted degree (ANOVA,  $df = 3, 103, F = 0.03, p = 0.99$ ), indegree centrality (ANOVA,  $df = 3, 103, F = 0.10, p = 0.95$ ), or outdegree centrality (ANOVA,  $df = 3, 103, F = 0.64,$

$p = 0.59$ ), indicating that the amount of time a fish was held prior to being assayed had no effect on behavior.

## Assessment of swimming performance

Swimming performance of bluegill was conducted in the 2 days following the conclusion of the social behavior assay, using a Brett-style swim tunnel (Brett 1964; Reidy et al. 2000; Tierney 2011). In this apparatus, fish were placed in a rectangular chamber within an acrylic racetrack, and current was subsequently forced through the chamber via a propeller attached to an electric motor. Swimming performance was then assessed by adjusting the current and determining the velocity at which the fish was no longer able to continue swimming (Brett 1964). Food was withheld from fish for 2 days prior to the swim performance test to ensure that performance differences between fish were not impacted by differential energetic demands induced by digestion (Pang et al. 2010; Rouleau et al. 2010). The chamber within the swim tunnel where fish were placed for assessment was 45 cm long, with a cross-sectional area of 209 cm<sup>2</sup>. Water temperature in the swim tunnel was maintained between 17 and 18 °C using a TK-500 Heater-Chiller (Teco®, Ravenna, Italy), and oxygen saturation was kept near 100% with an air compressor and air stone.

Swimming performance, defined as the fish's critical swimming speed,  $U_{crit}$ , was evaluated for 15 fish each day, such that all evaluations for all 30 fish in each set were completed over 2 days. For each trial, a single fish was quickly netted from its holding tank, identified via PIT tag, measured for total length, and placed within the chamber of the swim tunnel where it was initially forced to swim at a speed equal to 1 body length per second for 5 min to acclimate (Plaut 2001), after which time water velocity within the tunnel was increased by 0.5 body lengths per second every 5 min (hereafter, referred to as steps) until the fish reached the failure threshold and could no longer sustain swimming (Castro-Santos 2011). Each bluegill was considered to have reached the failure threshold when it was pushed by the current to the back of the chamber and its caudal fin was in contact with the rear grate of the chamber for a period of 4 s (Prenosil et al. 2016). When failure was reached before the end of a 5-min step,  $U_{crit}$  was calculated according to the following equation (Brett 1964):

$$U_{crit} = u_1 + (t_1/t_2 \times u_2)$$

where  $u_1$  is the highest speed (in cm s<sup>-1</sup>) that a fish could sustain for the full 5-min step,  $u_2$  is the speed at which failure was reached,  $t_1$  is the time swam within the step where failure was reached, and  $t_2$  is the total time of each step (5 min). While the length of time for each step before increasing the speed in the tunnel is shorter than in some prior studies of salmonids

(Gregory and Wood 1998; Reidy et al. 2000), we argue that a shorter step time was more ecologically relevant given the fact that bluegill do not usually occupy areas such as fast-flowing streams, or engage in long-distance swimming or migration that require long-term endurance (Jones et al. 2007). Upon failure, each bluegill was removed from the swim tunnel, weighed, and temporarily placed in a separate holding tank before being stocked into the 0.04-ha angling pond (see below). A total of 119 fish were stocked into the angling pond, with one fish dying in its holding tank prior to swim performance assessment.

### Angling trials

Angling trials were conducted in a single 0.04-ha angling pond and consisted of a series of nine angling sessions conducted over 2 weeks. The angling pond featured natural macrophyte cover and macroinvertebrate forage items and was also stocked with juvenile mosquitofish *Gambusia* spp. to serve as additional forage. By including a combination of forage items in the angling pond, we presumed that all bluegill were able to forage effectively. Angling was conducted daily from 6 June to 10 June, and again from 12 June to 15 June 2017. Each angling day included a single session that was conducted either in the morning (8:00 a.m.), midday (12:00 p.m.), or evening (4:00 p.m.) as determined by random selection. Each session was standardized to 45 total casts that, depending on the number of fish caught in the session, took between 45 min and 1 h to complete. All angling sessions were carried out by the lead author, who systematically moved around the entire perimeter of the pond during each session and casted in a way to ensure that all areas of the pond were targeted. The use of only a single angler, as opposed to multiple anglers, was done to avoid potential confounding effects of angler skill and approach on which fish were captured. Gear consisted of a light-action spinning rod spooled with 1.8 kg test Berkely Trilene™ monofilament fishing line, a setup commonly used by bluegill anglers. The bait used was a simple size 8 Gamakatsu® J-hook baited with a live waxworm *Galleria* spp. suspended in the water 1–1.5 m below the surface with a stationary slip bobber. Strikes were detected by watching the slip bobber on the surface and setting the hook when the bobber was pulled beneath the surface by the fish, a common practice for capturing bluegill. If no strike was detected within 1 min of casting the bait into the water, the bait was retrieved and subsequently casted into another location in the pond. Upon capture, each fish was quickly dehooked, identified using a hand-held PIT reader, and immediately released back into the pond to be potentially recaptured. Handling time for each captured fish was under 1 min, with no fish showing signs of bleeding or other disturbance upon release. The angling pond was drained approximately 1 month

after the conclusion of angling trials on 17 July, and 107 bluegill were recovered.

### Statistical analysis

While normalized social network metrics were calculated for all 120 fish, analyses relevant to vulnerability to angling were performed only on the 107 fish recovered from the angling pond. To reduce the social network data to functional components and eliminate issues of multicollinearity (Scheiner and Gurevitch 2001; Graham 2003), principal components analysis (PCA), based on the correlation matrix, was performed on the three measures of social behavior (weighted degree, indegree centrality, outdegree centrality), following evaluation of the suitability of the data for factor analysis (Hair 2010) (Kaiser–Meyer–Olkin test of sampling adequacy = 0.573, Bartlett’s test of sphericity,  $p < 0.001$ ). Varimax-rotated components with eigenvalues greater than 1 were retained based on the maximum likelihood solution (Kaiser 1960). Pearson correlations were performed to determine if  $U_{crit}$  or fish length was associated with extracted social metrics.

In order to test whether the overall catchability changed across all fish over the nine angling sessions, we ran a zero-truncated negative binomial regression that included session number as the explanatory variable and the number of captured bluegill in each session as the dependent variable. In order to assess whether social components, fish length, and/or swimming performance impacted vulnerability to angling in bluegill, we ran a pair of Cox proportional hazard models. In the first, we included these three factors as fixed covariates, with the session in which a fish was captured as the “mortality event.” For the second, we were interested in if any of these factors would cause a fish that had been already captured to be more likely to be captured again. For this model, we only included fish that had been captured at least once, included the same three covariates as in the first model, and set the session in which a fish was captured for the second time as the “mortality event.” In each model, we initially included all possible two-way interactions between covariates; however they were all removed after none of them proved to be significant.

All statistical analysis were performed using R Version 3.6.0, utilizing the packages ‘VGAM’ (Yee 2010), ‘Hmisc’ (Harrell et al. 2019), MASS (Venables and Ripley 2002), ‘survival’ (Therneau 2000), and ‘AER’ (Kleiber and Zeileis 2008). Thresholds for statistical significance in all cases were set at  $\alpha \leq 0.05$ , and all data are reported as means  $\pm$  standard error of the mean where appropriate.

## Results

Individual bluegill showed tremendous variation in their behavior during the social behavior assay. For the number of aggressive acts initiated, fish ranged from 0 to 285 attacks, while ranging in the number of acts received from 0 to 315 over the 3 days of observation (Table 1). Individual bluegill also varied in their propensity to associate with other individuals, with a range between 4 and 94% with regard to the percentage of observation points where a fish was within one body length of at least one other fish (Table 1).

Following principal components analysis on the three social network metrics, only a single component (hereafter, the “social score”) was extracted. The social score was positively loaded for indegree centrality and weighted degree, negatively loaded for outdegree centrality, and accounted for 68.4% of the total behavioral data variance (Table 2). Individuals with high outdegree centrality had low indegree centrality and low weighted degree, indicating that more aggressive individuals received fewer attacks and spent less time associating with other individuals.

Among the 107 bluegill recovered from the angling pond,  $U_{crit}$  ranged from 33.8 to 79.3 cm s<sup>-1</sup>, with a median of 57.9 cm s<sup>-1</sup> (Table 1). Neither social score ( $r = -0.086$ ,  $df = 105$ ,  $p = 0.37$ ) nor fish length ( $r = -0.084$ ,  $df = 105$ ,  $p = 0.38$ ) was related to  $U_{crit}$ , suggesting that swimming performance is not a driver of social rank in bluegill (Fig. 1). Bluegill total length and social score were also not correlated with each other ( $r = 0.025$ ,  $df = 105$ ,  $p = 0.79$ ), which was expected given that all social data were normalized to be relative to each individual’s shoalmates, and members of each shoal were of similar length.

Nine angling sessions resulted in a total of 90 capture events. In 25 additional cases, a strike was detected, but the fish was not successfully landed, resulting in an angler efficiency (78.2% of strikes were converted into captures) similar to previously published work examining links between behavior and angling vulnerability in fish (Louison et al. 2017). Twenty-six bluegill were captured during session 1 (Fig. 2) and capture rate declined with each subsequent session ( $z = -$

3.56,  $p < 0.001$ ). Of the 107 bluegill recovered following angling, 28 fish were not captured, 68 fish were captured once, and 11 fish were captured twice. The first recapture of a fish occurred during session 3, and no more than 1 recapture occurred in any subsequent session except for session 7, when 7 out of the 14 captures were recaptures of previously captured fish.

Total length was significantly associated with vulnerability to angling (Table 3), with length significantly increasing the probability of being captured both initially (Fig. 3b) and a second time (Fig. 4b). While the effect of length was strong, it was based within a relatively narrow range, as the difference in length between captured and uncaptured fish was small (captured fish were approximately 0.5 cm longer on average than uncaptured fish).  $U_{crit}$  was also a significant driver of initial capture (Table 3), with higher  $U_{crit}$  associated with greater risk (Fig. 3a).  $U_{crit}$ , however, was not a significant driver of whether a fish was then captured a second time (Table 3). Social score, while not a significant determiner of whether a fish was captured initially, was a significant determiner of whether a captured fish was subsequently captured a second time (Table 3; Fig. 4a).

## Discussion

In the present study, individual sociability/aggression impacted the vulnerability of bluegill to angling. More specifically, bluegill with higher sociability and lower aggressiveness were more vulnerable to recapture after being caught before. This finding is a significant addition to our knowledge of the drivers of angling vulnerability, as to our knowledge, the only published study (besides earlier work on bluegill in our laboratory, Louison et al. 2018a) to quantify the impacts of sociability on vulnerability to capture in fish found that social network position did not predict angling vulnerability in blacktip sharks *Carcharhinus melanopterus* (Mourier et al. 2017). With regard to aggression, the present results show that less aggressive and more social bluegill are more vulnerable to angling (at least, as defined by being vulnerable to recapture),

**Table 1** Median, range, and interquartile ranges for social behavior, aggression, critical swimming speed ( $U_{crit}$ ), and total length for all 120 bluegill *Lepomis macrochirus* initially included in the study. Aggressive acts given and received represent the sum over the 3 days of the social

Metric	Median	Range	Interquartile range
Length (cm)	17.6	14.9–19.4	17.3–18.1
No. of aggressive acts given	6.5	0–285	0.25–54.25
No. of aggressive acts received	25.5	0–315	15.5–69.75
Proportion of time with another fish	0.53	0.04–0.94	0.32–0.75
$U_{crit}$ (cm s <sup>-1</sup> )	57.9	24.5–79.4	47.3–62.5

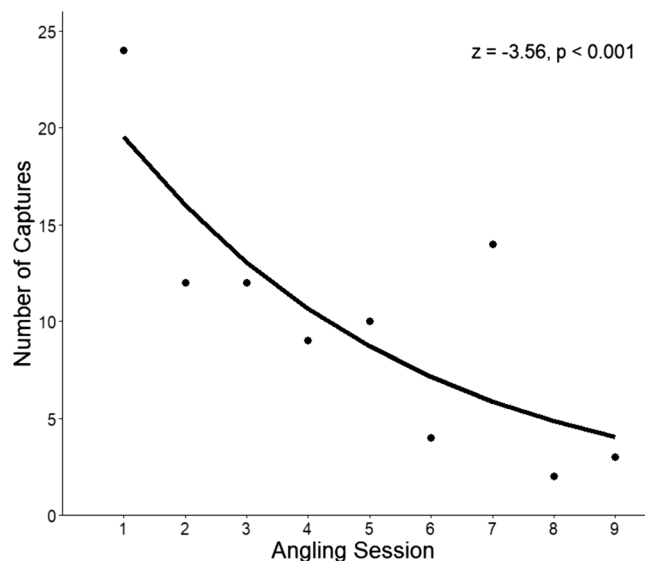
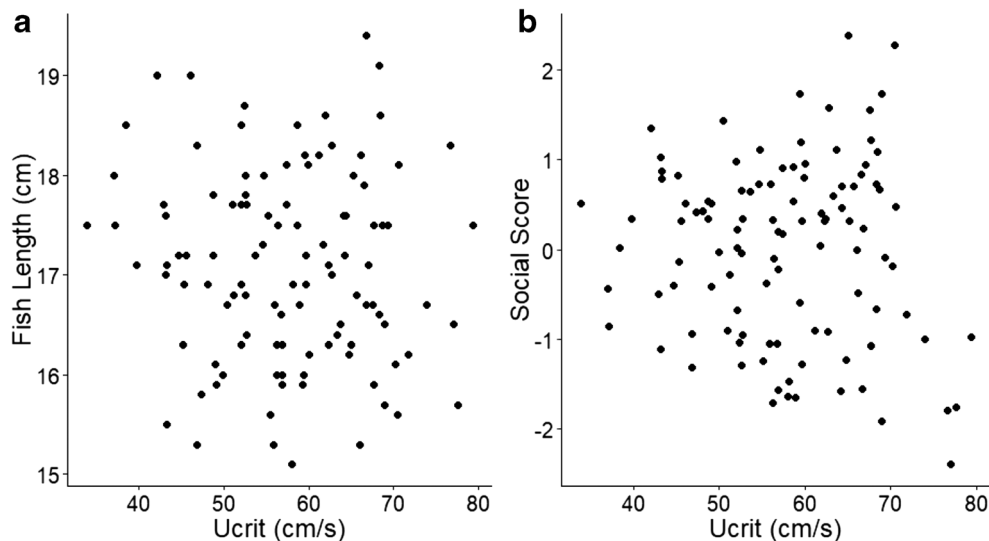
behavior assay, while proportion of time with another fish represents the proportion of observation points where a fish was within one body length of at least one other conspecific. For  $U_{crit}$  and length,  $N = 119$  as one fish died before swimming performance and length could be recorded

**Table 2** Factor loadings derived from principal components analysis (PCA) on the three social network metrics extracted from sociability trials in bluegill. Only a single component was extracted that included significant loadings for all three metrics; this component is hereafter referred to as the “social score”

Factor	PC1 loading
Indegree centrality	0.917
Outdegree centrality	-0.806
Weighted degree	0.749
Eigenvalue	2.052
% variance explained	68.4%

a result that runs contrary to previous work in other fish species (e.g., largemouth bass, *Micropterus salmoides*) where results have shown that aggressive and (presumably) bold phenotypes are the most vulnerable (Sutter et al. 2012; Arlinghaus et al. 2017b; Twardek et al. 2017). This could be due to the bait type we used in this study compared to the studies of other species. These previous studies relied largely on lures that were towed through the water, necessitating a fast and “aggressive” response to strike. In the case of the present study with a stationary lure, an aggressive response was likely not necessary to strike, and as such, higher aggression did not increase angling vulnerability. Rather than being based on an aggressive response, the mechanism driving the relationship between angling vulnerability and sociability may be related to the fact that social individuals are more likely to congregate in large groups within their environment, which likely impacts their interaction with angling lures (Jacoby et al. 2014; Öst et al. 2015). While forming groups increases foraging success for individuals within the group (Pitcher et al. 1982), it also increases competition for food among group members (Kent et al. 2006; Ward et al. 2006) requiring individuals to make

**Fig. 1** Relationship between swimming performance ( $U_{crit}$ , in  $\text{cm s}^{-1}$ ) and **a** fish length and **b** social score in bluegill. Swimming performance was not significantly related to either metric



**Fig. 2** Number of bluegill captured across the 9 experimental angling sessions. Total captures for each session include captures of fish for the first time, as well as recaptures (1 recapture in sessions 3, 4, 5, and 9; 7 recaptures in session 7). The number of fish captured declined significantly over the course of the sessions, as determined by a zero-truncated negative binomial regression

faster decisions regarding whether to feed on an available prey item (Stoner and Ottmar 2004). This process may extend to fishing lures as well, causing group-living individuals to be quicker to strike baited hooks and lures. Indeed, increases in fish density within small ponds have been shown to cause greater than expected increases in catch rates for angled fish, suggesting that each individual fish becomes more vulnerable as density increases, possibly as a result of this competition (Raat 1991; Härkönen et al. 2014). As a result, highly social bluegill that reside in larger groups may be less discerning when evaluating fishing lures as a potential prey item in a highly competitive social context, leading to greater



**Table 3** Output from Cox proportional hazard models assessing the impact of social score, swimming performance, and total length on vulnerability to angling in bluegill. In the first model, the initial capture of a bluegill is treated as the mortality event, with all available bluegill included ( $N = 107$ ). In the second model, only fish that had already been captured once were included ( $N = 79$ ), with the mortality event being when a fish was captured for a second time. In total, 28 bluegill were not captured at all, 68 bluegill were captured once, and 11 bluegill were captured twice

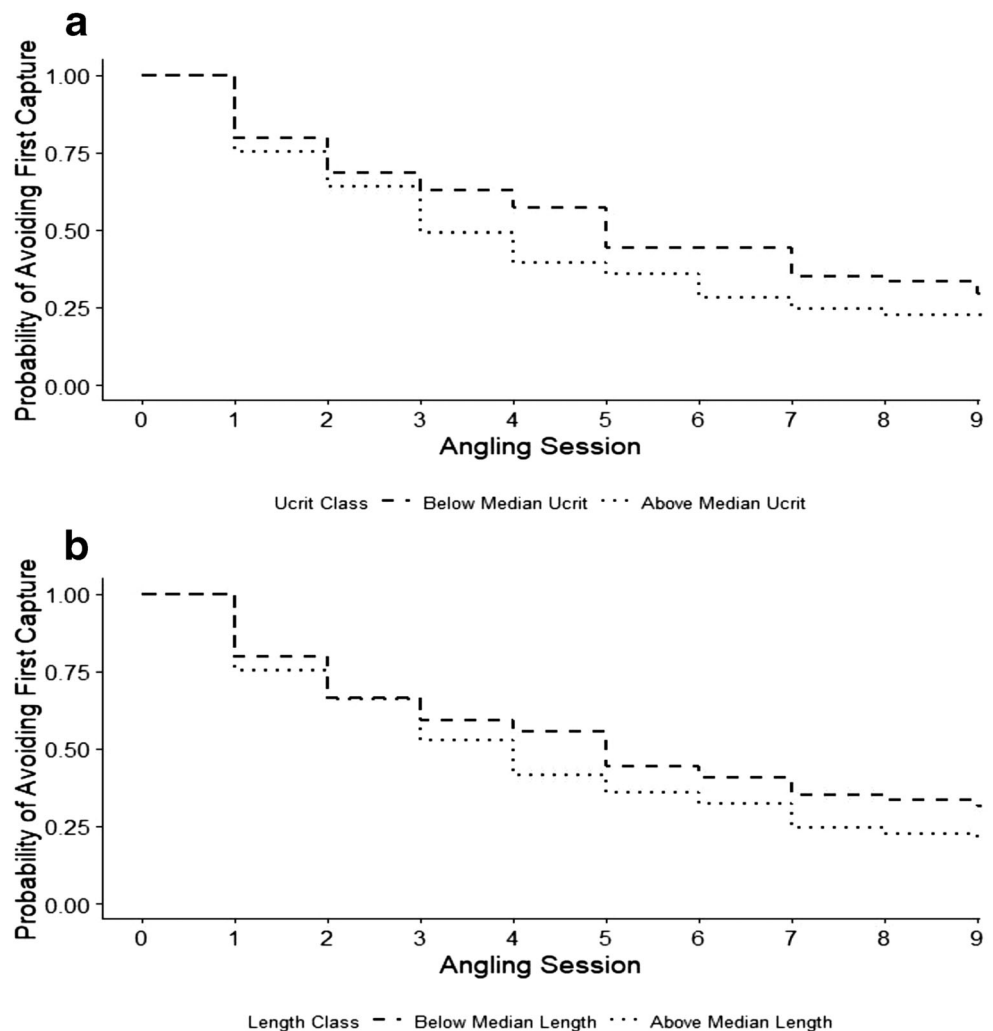
	Hazard ratio	S.E.	Z	p
For initial capture				
Social score	1.09	0.11	0.83	0.40
<i><math>U_{crit}</math> (<math>\text{cm s}^{-1}</math>)</i>	<i>1.55</i>	<i>0.20</i>	<i>2.12</i>	<i>0.03</i>
<i>Total length (cm)</i>	<i>1.50</i>	<i>0.13</i>	<i>3.07</i>	<i>0.002</i>
For second capture				
<i>Social score</i>	<i>2.23</i>	<i>0.35</i>	<i>2.23</i>	<i>0.02</i>
<i><math>U_{crit}</math> (<math>\text{cm s}^{-1}</math>)</i>	<i>2.41</i>	<i>0.61</i>	<i>1.43</i>	<i>0.15</i>
<i>Total length (cm)</i>	<i>2.27</i>	<i>0.38</i>	<i>2.13</i>	<i>0.03</i>

Significant factors are given in italics

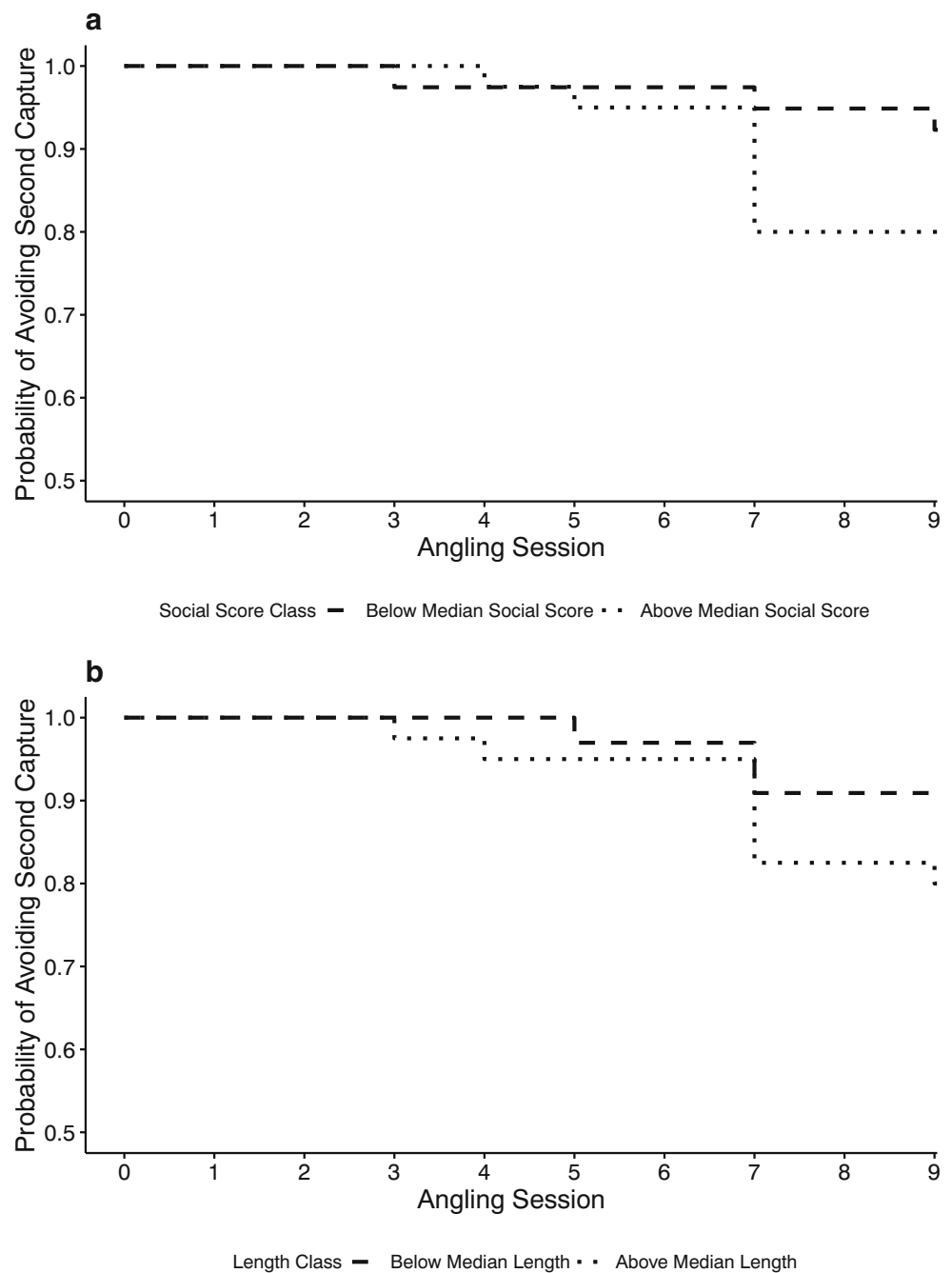
vulnerability. Furthermore, because fish are aware of the foraging activity of fellow group members (Pitcher et al. 1982), any bait that lands near any of the members in a group is likely to elicit a response from nearby group members, effectively increasing the “strike radius” for a fish in a group relative to a solitary fish.

Bluegill size was a predictor of angling vulnerability, with larger individuals being more likely to be captured as well as recaptured. It should be noted that, while the difference in total length between captured and uncaptured bluegill was rather small (captured fish averaged 17.2 cm and uncaptured fish averaged 16.8 cm, a  $\sim 3\%$  difference), selective capture of larger individuals within a small size range has been shown previously (Klefoth et al. 2017). Several prior studies in fish have additionally documented intraspecific size-selective harvest in freshwater systems (Vainikka et al. 2016; Arlinghaus et al. 2017a). Furthermore, intrinsic growth rate (independent of absolute fish size at capture) has also been linked with increased capture vulnerability previously (Biro and Post

**Fig. 3** Survival plots derived from a Cox proportional hazard model that tested whether social score, swimming performance, and/or fish length impacted whether a bluegill ( $N = 107$ ) was captured, and how many sessions took place before that event occurred. The plots are broken down based on **a**  $U_{crit}$  (in  $\text{cm s}^{-1}$ ) and **b** total length (in cm). Lines with different symbology represent fish that were either above (dotted) or below (dashed) the median value for the given metric



**Fig. 4** Survival plots derived from a Cox proportional hazard model that tested whether social score, swimming performance, and/or fish length impacted whether a bluegill that had already been captured ( $N = 79$ ) was captured a second time, and how many sessions took place before that event occurred. The plots are broken down based on **a** social score and **b** total length (in cm). Lines with different symbology represent fish that were either above (dotted) or below (dashed) the median value for the given metric



2008; Saura et al. 2010). As such, greater vulnerability of larger bluegill in the present study may be related to growth rate, where faster growers have higher feeding rates (Stamps 2007) and, as a result, are more likely to prey upon a baited hook. Because the bluegill in the present study were not aged, however, and were raised in a natural environment where they were not separated by spawning cohort, this possibility cannot be proven as larger fish could have simply been older, and not necessarily faster growers per se. Alternatively, selective capture of larger bluegill in the current study could be a product of gape size, where larger individuals with increased gape size

are better able ingest lures, facilitating capture, while smaller fish may be more likely to “nibble” the bait rather than ingesting it completely (Alós et al. 2014). Indeed, previous studies have shown the traits that make fish more likely to encounter and decide to strike a lure or bait are not sufficient to explain individual angling vulnerability, as the ability to ingest the gear is critical as well (Lennox et al. 2017; Monk and Arlinghaus 2017). Given the fact that total length ranges of uncaptured fish overlapped with those of captured fish (i.e., there did not appear to be a cutoff where all fish below a certain total length were not captured), this appears unlikely

to be the only explanation for the present results. Finally, because larger fish within centrarchid groups tend to assume dominance (Beacham 1988; Dugatkin and Ohlsen 1990), it is possible that larger bluegill were simply able to dominate areas of foraging space and force smaller fish to more peripheral habitats and, in turn, were more likely to encounter baited hooks. This behavioral explanation also seems unlikely though, given the fact that more aggressive individuals were clearly not more vulnerable to capture (whether initial capture or recapture), and also that efforts were made to cast lures to all areas of the pond to eliminate habitat bias in capture. Within this experimental construct, it was found that larger bluegill were more vulnerable to angling, albeit within a relatively narrow size range.

Swimming performance, as measured by an individual's critical swimming speed, was significantly and positively associated with the likelihood of initial capture. Swimming performance is a highly repeatable physiological trait in fish, albeit one that can be impacted greatly by conditions, such as food availability or temperature (Gregory and Wood 1998; Reidy et al. 2000; Pang et al. 2016). While swimming performance was related to initial angling vulnerability, it was not related to any aspect of social behavior, a different finding than what has been shown previously (Killen et al. 2017). This lack of a relationship likely reflects the biology of bluegill, as while bluegill form large aggregations around available resources, they do not typically form highly structured schools that travel for long distances (McCartt et al. 1997), which would necessitate social structuring based on individual performance (Killen et al. 2017). For angled bluegill, the mechanism driving the relationship between swimming performance and angling vulnerability is unclear; however, we speculate that, as all the fish are initially looking to feed upon the baited hook, it could simply be that better swimmers are quicker to reach it and are thus more vulnerable. While prior work has examined the relationship between swimming performance and feeding rate (independent of angling), the results have been somewhat inconsistent. In one study of common carp *Cyprinus carpio*, fish with higher  $U_{crit}$  also had higher feeding rates and, in turn, growth rates; however, this relationship disappeared when fish were assessed at low temperatures (Pang et al. 2016). Conversely, a study of rainbow trout *Oncorhynchus mykiss* found that higher  $U_{crit}$  was associated with lower rates of food consumption when fed satiation rations (Gregory and Wood 1999). Regardless of the mechanism at play here, another aspect of these findings is that while  $U_{crit}$  significantly predicted initial capture, its influence on vulnerability changed as angling sessions progressed, as it did not significantly impact whether a fish was recaptured. This could reflect a change in how fish, especially fish that had already been captured, view the baited hook following experience. Indeed, numerous studies have indicated that the vulnerability of fish is at its highest point when they are totally naïve to capture (Young and Hayes 2004; Askey et al. 2006; Arlinghaus et al. 2017a; Louison et al. 2017; Koeck et al.

2019) and that fish that have been previously hooked become much more wary of anglers (Lennox et al. 2016). Under initial conditions, the baited hook may be seen as an easy food source and the “free for all” conditions may predispose large, fast swimming bluegill to higher vulnerability. However, after learning takes place, bluegill become more wary of lures, and at that point, it is not swimming performance but rather social behavior that makes a fish more likely to be captured a second time. Collectively, these results demonstrate that the definition of angling vulnerability may not be simple, and that under different circumstances, different characteristics are likely to be drivers of vulnerability in an individual. In turn, this means that the traits that drive selective capture are not likely to be static, and will likely change depending on the degree of exposure angled populations receive to angling pressure.

The results of the present study highlight a key factor that may impact the selectivity of angling based on behavior and physiology, which is the bait used and its overall effectiveness. While several previous studies have documented selection where traits such as higher boldness and exploratory behavior, aggression, activity, and metabolic rate (i.e., traits associated with a “fast” life history, see Biro and Stamps 2008; Binder et al. 2016) render a fish more vulnerable (Redpath et al. 2010; Härkönen et al. 2014; Villegas-Rios et al. 2014; Hessenauer et al. 2015), it should be noted that these studies targeted fish with a variety of artificial lures or baits that were retrieved rather than being allowed to remain motionless, as was the case in this study. Indeed, previous work has shown that more stationary baits tend to catch shyer individuals compared to actively retrieved lures in multiple fish species (Wilson et al. 2015). Not only did the present study involve a stationary lure, but it also involved live bait as opposed to an artificial bait or plastic lure, and prior work has also shown that the type of bait on a hook may impact what behaviors are selectively captured, even with everything else about the angling approach (line, retrieval speed, etc.) kept equal (Härkönen et al. 2016). The use of natural bait in the present study also likely impacted how vulnerability to angling was defined relative to our previous work with bluegill (Louison et al. 2018a). In that study, a similar gear was used (stationary hook below a float); however, artificial bait was utilized instead of natural bait, which has been shown previously to capture a smaller proportion of available fish (Härkönen et al. 2016) and did again here (40 of the 151 available fish were captured at least once in Louison et al. 2018a, compared to 79 of the 107 bluegill in the present study). This may well account for the somewhat discordant results of the present study with regard to sociability (as sociability did not predict whether a fish was captured at least once). In the previous work, the most vulnerable fish had only been captured once (and were more social) with the median fish left uncaptured, and only one fish was captured twice. In the present study, the median fish had been captured once with only a minority of fish left uncaptured, while 11 fish were captured twice and could be considered the most vulnerable to angling. In this context, the

finding that sociability led to a greater likelihood of recapture actually is similar to the results of Louison et al. (2018a), namely that more social bluegill are likely to be the most vulnerable to angling in a given population, regardless of how effective the angling was. The collective results of these studies, as well as earlier studies of angling vulnerability, therefore emphasize the fact that the results of selection experiments are often not generalizable and may return disparate results depending on bait type, species, and the overall effectiveness of the gear.

The results of this study are applicable to the overall study of how fished populations respond evolutionarily to selective capture. While evolutionary changes to life history traits (growth, reproductive age, etc.) have been well documented in fish (Kuparinen and Merilä 2007; Kuparinen and Hutchings 2012; Heino et al. 2015), recent work has shown that behavioral and physiological traits may evolve in freshwater sportfish populations as well due to selective harvest (Uusi-Heikkilä et al. 2008; Philipp et al. 2009; Leclerc et al. 2017). With regard to this question, however, it is difficult to make definite predictions about the evolutionary impact of selective angling harvest on bluegill based on the present findings. While larger size was a driver of capture regardless of how it was defined, swimming performance only predicted the initial capture, while social behavior only predicted recapture. On one hand, bluegill are a sought-after sportfish for anglers looking to harvest fish to consume (Reed and Parsons 1999; Paukert et al. 2002), meaning that only the traits leading to initial capture could be under selection if captured fish are likely to be harvested. However, research shows that a substantial proportion of angled bluegill are eventually released (over 90%, Gaeta et al. 2013). This means that the traits that render a fish more likely to be captured multiple times may be important from a selection perspective, as fish that are caught once and subsequently avoid capture are, in all likelihood, less likely to suffer angling-related mortality than fish that continue to strike baits even after previously being captured, as each new capture event freshly exposes a fish to the risk of either harvest or post-release mortality due to capture and handling stress (Cooke and Suski 2005; Gingerich et al. 2007). Furthermore, the present results are complex in that, if evolution favoring less social and more aggressive phenotypes is occurring in bluegill, they run somewhat in opposition to a predicted “timidity syndrome” in fish stocks subjected to intense angling pressure, as bolder and more aggressive individuals are removed (Arlinghaus et al. 2017b). This finding is consistent with previous results in bluegill (Louison et al. 2018a), further demonstrating the importance of individual sociability in driving angling vulnerability for this species. In addition, Wilson et al. (2011) found that angled bluegill were shyer than those seined from the same location, indicating that bold and aggressive individuals are not more vulnerable to angling, at least for this species. The lack of selection favoring these “slow life history” traits in this species likely reflects not only the behavioral traits of bluegill, but also the angling methods used to target them. Going forward, the

only way to know with certainty the evolutionary impact of angling on this species will be to monitor the behavior and physiology of bluegill in the wild and use this information to determine if the outcome of these selection experiments is actually predictive of evolution in exploited populations.

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**Data availability** The datasets generated and/or analyzed during the current study are not publicly available because some of the data may still be used for a subsequent manuscript, but are available from the corresponding author on reasonable request.

## Compliance with ethical standards

**Ethical statement** All experimental procedures were approved by and conducted in accordance with the University of Illinois Institutional Animal Care and Use Committee (IACUC), protocol #16039. All applicable national and/or institutional guidelines for the use of animals were followed. All aspects of the manuscript were produced by the authors, with no permission needed for any material from other parties.

**Conflict of interest** The authors declare that they have no conflict of interest.

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