

ARTICLE

Largemouth bass use prior experience, but not information from experienced conspecifics, to avoid capture by anglers

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Abstract

Angler satisfaction is based on the presence of catchable fish, and therefore, understanding the mechanisms driving catchability is important for fisheries biologists and managers. Lure avoidance learning (including *via* social learning) may be a driver of catchability, but these mechanisms have not been explored in depth. To address this, largemouth bass, *Micropterus salmoides* (Lacépède), were stocked into four ponds, and two were angled using a green plastic worm. Naïve bass were then introduced into all ponds, and angling commenced using a sequence of three lures (green plastic worm, white plastic worm and in-line spinnerbait). Naïve bass stocked alongside experienced conspecifics were not less catchable, indicating socially learned lure avoidance did not take place. Catch rates declined across sessions until the switch to the spinnerbait, when rates temporarily spiked. This suggests that the similarity of a novel lure to previously experienced lures may determine if a fish avoids angling capture.

KEYWORDS

angling vulnerability, fisheries-induced evolution, lure avoidance, predator avoidance, search image, social learning

1 | INTRODUCTION

Learning is essential for survival, as organisms must glean information from their environment to forage successfully, attract mates and avoid predators (Brown & Laland, 2003; Lima & Dill, 1990). The ability to learn is therefore linked to fitness outcomes whereby individuals that successfully acquire and incorporate new information into behavioural decisions will likely experience greater fitness (Griesser & Suzuki, 2017; Manassa & McCormick, 2013; Sih & Del Giudice, 2012). This need to acquire and process information is also important in environments altered by human activities, including the destruction of habitat, hunting and fishing, pollution, or the introduction of non-native species (Sih, 2013). These rapidly changing environments present situations in which individuals must learn to alter their behaviour to avoid novel threats and take advantage of novel resources (Sih, Trimmer, & Ehlman, 2016; Wong & Candolin, 2015). During this process of adjusting their behaviour, individuals must also learn to

identify novel cues that indicate danger, such as visual or olfactory cues given off by novel predators, and avoid responding to these cues in an inappropriate way (Bouwman & Hawley, 2010; Chitwood, Lashley, Moorman, & DePerno, 2017). Accurately assessing new cues in the environment, and discerning between novel threats to be avoided and novel resources to be exploited, is therefore crucial to survival in environments altered by human activity.

Direct experience with non-lethal threats can result in learning, ultimately leading to effective threat avoidance in the future (Askey, Richards, Post, & Parkinson, 2006; Brown et al., 2011; Ferrari, Gonzalo, Messier, & Chivers, 2007). Examples of direct learning by animals include the avoidance of flower colours associated with predatory threat by bumblebees *Bombus terrestris* (Dawson & Chittka, 2014), avoidance of an electric shock by learning to associate the shock and a flashing light by guppies *Poecilia reticulata* Peters (Budaev & Zhukov, 1998), and linking the presence of a model predator with predator odour by Arctic charr, *Salvelinus alpinus* L.,



(Vilhunen, Hirvonen, & Laakkonen, 2005). In each of these cases, a single cue was associated with a particular threat. In nature, however, individuals are constantly bombarded with a host of cues that must be deciphered to formulate an appropriate behavioural response (Bourdeau, Pangle, Reed, & Peacor, 2013; Stamps & Frankenhuis, 2016). The ability to generalise cues to avoid novel threats that are similar to familiar threats can therefore enhance survival probability (Sih et al., 2010), and individuals that fail to avoid a novel threat (Blake, Alberici da Barbiano, Guenther, & Gabor, 2015; Kuehne & Olden, 2012) often do so when the novel threat is highly dissimilar from previously experienced threats (Trimmer, Ehlman, & Sih, 2017).

In addition to learning through direct experience, individuals can learn *via* social interactions with conspecifics (Griffin, 2004). This "social learning" can facilitate a far more rapid spread of information among individuals than if direct experience was necessary for learning (Aplin et al., 2015; Page & Ryan, 2006). Social learning can occur by direct observation of conspecifics at the moment they deal with a threat cue, or indirectly through interactions with conspecifics with previous experience with a threat cue (Arai, Tominaga, Seikai, & Masuda, 2007). In addition, this social learning can be accomplished through several mechanisms, for instance through social facilitation where a demonstrator's presence facilitates enhanced learning, local enhancement where a demonstrator directs an observer to a place where learning can occur, as well as observational conditioning where an observer is able to monitor a demonstrator's response to a stimulus to form a connection between the demonstrator's response and the stimulus (Rendell et al., 2011). While the various modes of social learning are often associated with higher vertebrates, numerous studies have shown that social learning occurs in a host of animal taxa, including fish (Brown & Laland, 2003). For example, Japanese flounder, *Paralichthys olivaceus* (Temminck & Schlegel), successfully learned to avoid a predator by watching other flounder being preyed upon (Arai et al., 2007). Being in the presence of experienced individuals also facilitated improved avoidance behaviour in naïve guppies escaping a model trawl net (Brown & Laland, 2002), and naïve fishes have been shown to learn more quickly to associate predator odours with danger when they were placed together with individuals experienced with that predator (i.e. through observational conditioning, Crane, Mathiron, & Ferrari, 2015; Manassa & McCormick, 2012). Social learning has also been implicated in the avoidance of capture by humans engaged in recreational fishing. For example, lined bristletooth, *Ctenochaetus striatus* (Quoy & Gaimard), that had never been targeted by spearfishers were quicker to flee when residing in locations where other species were targeted, presumably as a result of watching individuals from targeted species being speared (Tran, Langel, Thomas, & Blumstein, 2016). The use of social learning (regardless of the mechanism) could facilitate the rapid spread of effective behavioural strategies to avoid the threat of capture via recreational angling. More broadly, capture by humans in the context of hunting or fishing presents a novel threat in which learning may ameliorate predation risk and increase the likelihood of survival.

Recreational fishing is a multi-billion dollar industry worldwide and serves as a major economic driver for many communities

(Arlinghaus et al., 2016; Hunt, Arlinghaus, Lester, & Kushneriuk, 2011). Studies suggest that extensive recreational fishing harvest can result in the decline or collapse of populations of many targeted species (Post, 2013; Post et al., 2002). For fish populations, one way of avoiding extensive harvest is to learn to avoid fishing lures. For example, catch rates of northern pike, *Esox lucius* L., have been shown to drop in response to previous angling pressure, presumably due to learning (Arlinghaus, Alós, Pieterek, & Klefoth, 2017; Kuparinen, Klefoth, & Arlinghaus, 2010). Lure avoidance learning in this species has been found to be especially rapid for artificial lures such as spinnerbaits as opposed to live bait (Beukema, 1970). Indeed, declines in catch rates as fish learn to avoid baits and lures have been shown in several species, including common carp, *Cyprinus carpio* L. (Beukema, 1969; Klefoth, Pieterek, & Arlinghaus, 2013), rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Askey et al., 2006; van Poorten & Post, 2005), largemouth bass, *Micropterus salmoides* (Lacépède) (Philipp et al., 2009; Wegener, Schramm, Neal, & Gerard, 2018), brown trout *Salmo trutta* L. (Young & Hayes, 2004) and painted comber, *Serranus scriba* (L.) (Alos, Palmer, Trias, Diaz-Gil, & Arlinghaus, 2015). Furthermore, the application of constant angling pressure may reduce the catchability of fish by selecting for individuals that can better avoid capture, leading to evolution (Hessenaue, Vokoun, Davis, Jacobs, & O'Donnell, 2016). It should be noted also that lure avoidance learning does not seem to be permanent, as the catchability of fish has been shown to increase after temporary drops in angling pressure (Camp, van Poorten, & Walters, 2015). Clearly, fish are able to learn to avoid angling capture effectively with cumulative angling pressure, but the exact mechanisms of that learning are still not defined.

Potential learning mechanisms driving lure avoidance include social learning, as well as the transfer of knowledge from one lure that the fish has experienced to a novel lure type. Prior angling experiments have found various results with regard to the possibility of social learning. While Beukema (1969) found that catch rates of common carp declined even when fish were only hooked and not captured, indicating social learning, Wegener et al. (2018) found no drop in the catch rates of uncaptured largemouth bass as angling progressed, indicating that social learning may not have occurred in this species. With regard to generalising prior lure experience to new lures, Lennox et al. (2016) found that Atlantic salmon, *Salmo salar* L., were more likely to be recaptured on a novel lure than the lure on which they were originally captured, indicating that fish may successfully learn to avoid one lure without gaining less vulnerability to another. However, this study did not examine whether lure avoidance learning might be generalised depending on the degree of similarity between lures the fish has experienced and lures it has not, as it examined the response to different gear types (flies vs artificial lures vs live baits). An enhanced understanding of the behavioural mechanisms driving lure avoidance will inform predictions regarding the alteration of fish behaviour with increased exposure to recreational angling. In addition, research into this topic could be generalised to additional situations in which animals are impacted by

human activity, to define better the learning mechanisms necessary to survive in such environments.

The goal of this study was to test the hypothesis that fish that are naïve to angling experience social learning from conspecifics that have experienced angling, resulting in a difference in catch rates. Specifically, the interest was on observational conditioning, one of several types of social learning mechanisms that have been demonstrated in animals (Rendell et al., 2011). This specific form of social learning involves the use of public information (i.e. information that is freely available to all members of a group and is not directed by a demonstrator to a specific observer) and would presume that fish using this information are attentive to how others in the group are reacting to stimuli, including the appearance of a fishing lure (Danchin, 2004; Rendell et al., 2011). In addition, the study aimed to determine if fish are able to avoid novel lures based on the degree of similarity between a novel lure and previously experienced lures. While previous work has posited that social learning of lures does not occur in largemouth bass (Wegener et al., 2018), this study did not explicitly control the angling experience of all individuals, and because it used numerous lures, it is difficult to determine the degree to which social learning-based avoidance may or may not take place on a given lure type. To test these learning mechanisms more explicitly, an angling-naïve population of hatchery-raised largemouth bass *Micropterus salmoides* was used. In addition to being easy to hold in captivity, largemouth bass were used in this study because this species is among the most popular recreational angling targets in all of North America (Gaeta, Beardmore, Latzka, Provencher, & Carpenter, 2013) and has been extensively studied in the context of vulnerability to capture via recreational angling (Hessenauer et al., 2015; Louison, Adhikari, Stein, & Suski, 2017; Philipp et al., 2009). Upon completion, the results from this study will develop understanding of the role learning plays in angling vulnerability and which mechanisms are used by largemouth bass to avoid capture.

2 | METHODS

2.1 | Experimental fish and pond holding

On 10 May 2017, 312 largemouth bass (mean total length \pm standard error of the mean (SEM) = 177.7 \pm 0.6 mm) were acquired from Keystone Fish Hatchery in Richmond, IL, USA and transported to the Illinois Natural History Survey's Aquatic Research Facility in Champaign, IL, USA, where experiments were conducted. Upon arrival, 160 fish were haphazardly selected as "demonstrator" fish, implanted with a passive integrated transponder (PIT) tag for identification and stocked into a series of four small (0.04 ha), rectangular, earthen bottom ponds at a density of 40 fish per pond (Figure 1). The remaining 152 fish were stocked into a single large (0.12 ha) holding pond for future use as "observer" fish. Each small angling pond, as well as the larger holding pond, was stocked with fathead minnow, *Pimephales promelas* (Rafinesque), to serve as forage. Across all angling sessions, temperature in the ponds varied with ambient conditions between 22.8 and 30.1°C (Mean

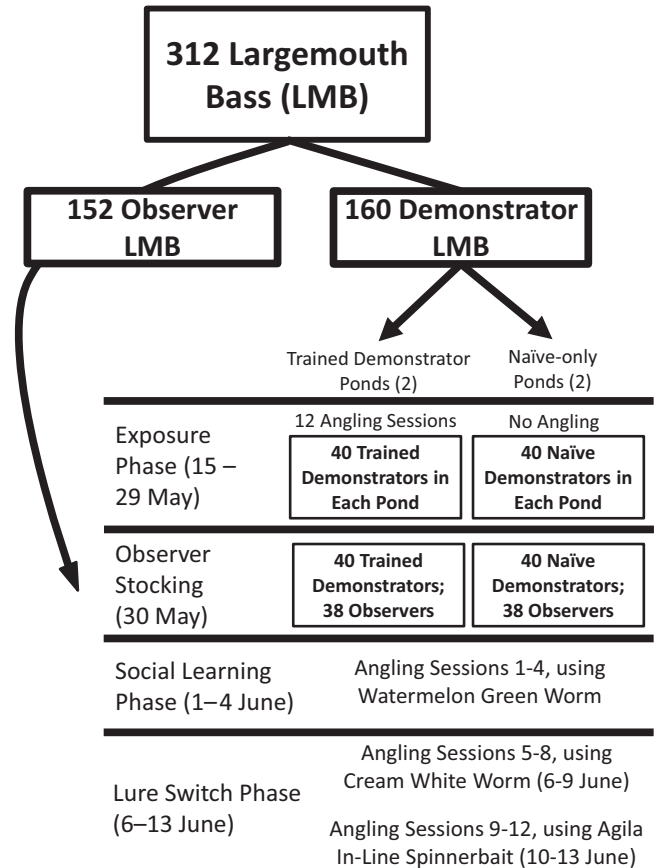


FIGURE 1 Flow chart detailing the overall experimental design for the four angling ponds containing largemouth bass

temperature \pm SEM = 26.6 \pm 0.27°C). Mean dissolved oxygen \pm SEM in the ponds over all sessions was 11.56 \pm 0.6 mg/L. All aspects of this study (including fish holding and subsequent angling) were conducted in accordance with the University of Illinois Institutional Care and Use Committee, Protocol #17065, in compliance with the U.S. National Research Council's Guide for the Care and Use of Laboratory Animals, the U.S. Public Health Service's Policy on Humane Care and Use of Laboratory Animals and the Guide for the Care and Use of Laboratory Animals.

2.2 | Study overview

This study was divided into three phases: an exposure phase, a social learning phase and a lure switch phase (summarised in Figure 1). The purpose of the exposure phase was to establish two ponds with trained demonstrators and two ponds with naïve demonstrators. No difference in fish size was present among angling ponds (ANOVA, $F = 2.38$, $p = 0.06$). During the exposure phase, angling was conducted for 12 days in the two ponds designated to hold trained demonstrators to provide those fish experience with angling. Following the conclusion of the exposure phase, observers were recovered from the holding pond and evenly stocked into the four angling ponds for a final density of 78 fish/pond (40 demonstrators and 38 observers). The purpose of the social learning phase was to assess

whether naïve observers learned to avoid lures *via* social learning from trained demonstrators by comparing observer catch rates with trained and untrained demonstrators. The social learning phase began two days later, whereby ponds were angled for four days, and the number of captures of observers held in ponds containing both trained and naïve demonstrators was recorded. This acclimation period between observer stocking and subsequent retesting is similar to laboratory studies examining how observers behave in the presence of demonstrators familiar with a certain threat or cue (Brown & Laland, 2002; Chivers & Ferrari, 2014; Lindeyer & Reader, 2010). The purpose of the lure switch phase was to determine if fish could generalise learned lure avoidance to a novel lure, and if that learning depended on the degree of similarity between the novel lure and a prior lure. Two days after the conclusion of the social learning phase, the lure switch phase began whereby all four ponds were angled for four days with a lure similar to the lure used in the exposure and social learning phases, and then for four additional days with a lure that was different from either of the lures used previously.

2.3 | Exposure phase

Angling during the exposure phase was conducted in two ponds over 12 days between 15 May and 29 May to generate trained demonstrator fish that had experience with angling. Concurrent with this were two identical ponds stocked at identical densities, but that did not receive angling to generate naïve demonstrators (Figure 1). Each angling day consisted of a 45-min angling session conducted by a single experienced angler (lead author MJL) between 8:30 and 18:30. During each angling session, the angler was free to move around the perimeter of the pond while making an effort to cast to all areas of the pond. Angling gear consisted of a medium action spinning rod spooled with 1.8-kg Trilene® clear monofilament fishing line. Terminal tackle consisted of a size 6 Gamakatsu™ octopus circle hook baited with a 7.6-cm watermelon-green coloured plastic worm (Yamasenko™, Gary Yamamoto Custom Baits) rigged “wacky” style (Figure 2). Once a strike was detected by the angler, the hook was immediately set and the demonstrator fish was quickly retrieved from the pond and its PIT tag number determined with a portable reader (Biomark®, Boise, ID, USA), after which the fish was released back into the same pond within one minute of landing. Upon the completion of the exposure phase on 29 May, the fish held in the two angled ponds were established as trained demonstrators, while the fish in the two ponds that did not receive angling were established as naïve demonstrators.

2.4 | Social learning phase

Angling during the social learning phase was conducted in all four ponds (two containing trained demonstrators plus observers, two containing naïve demonstrators plus observers) over four angling days between 1 June and 4 June, two days after the conclusion of the exposure phase (Figure 1). This phase consisted of four daily angling sessions (hereafter, sessions 1–4), each lasting 45 min. All four ponds

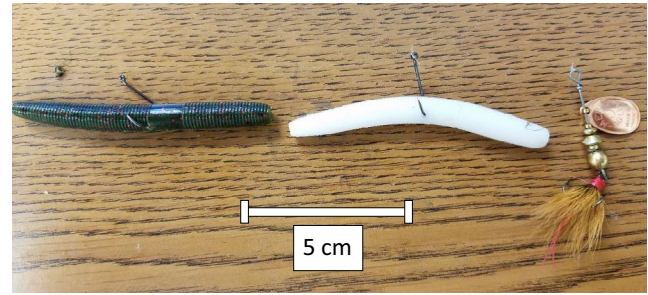


FIGURE 2 Photograph of lures used during angling. From L to R: Watermelon-coloured plastic worm, used in all training and social learning phase sessions; cream-white plastic worm, used in sessions 5–8 of the lure switch phase; and Agila spinnerbait, used in sessions 9–12 of the lure switch phase [Colour figure can be viewed at wileyonlinelibrary.com]

were angled daily such that one pond containing observers/naïve demonstrators and one pond containing observers/trained demonstrators were angled between 07:45 and 11:15, while the remaining two ponds were angled between 13:00 and 17:15. The timing (morning/afternoon) and sequence the ponds were angled each day was initially determined randomly and alternated daily thereafter so that each pond was angled twice in the morning and twice in the evening during the 4 days of social learning phase. Angling sessions were conducted in a manner identical to the exposure phase, except that, for this portion of the study, two anglers were responsible for carrying out all angling, with one angler fishing the morning sessions and the other fishing the afternoon sessions, as determined by random selection. It was necessary to use two anglers for this portion of the study to ensure that all angling sessions could be completed within the timeframe set for the study. Differences between anglers in angling effort and capture rates were quantified by recording the number of casts attempted during each session, as well as the number of times the angler felt a strike but was unable to successfully land the fish.

2.5 | Lure switch phase

Angling during the lure switch phase was conducted in all four ponds over eight angling days between 6 June and 13 June, beginning two days after the completion of the social learning phase (Figure 1). Angling sessions were scheduled in a manner identical to the social learning phase whereby two ponds were fished in the morning and two ponds fished in the afternoon on each angling day. During the first four lure switch angling sessions (sessions 5–8, from 6 June–9 June), a cream-white plastic worm replaced the watermelon-coloured plastic worm used in the previous two phases of the study (Figure 2). This lure was exactly the same in model, size and how it was rigged as the first lure, the only difference being its colour. During the final four angling sessions (sessions 9–12, from 10 June–13 June), a size 0 Mepps® Agila model in-line spinnerbait was used (Figure 2). This lure was different in colour, shape and retrieval speed than the previous lures (Figure 1), which allowed for an assessment of whether fish could



successfully avoid a novel lure type as a result of prior experience with dissimilar lures.

2.6 | Statistical analysis

To determine if catchability changed for trained demonstrators during the exposure phase, a Poisson regression was run that included session number as a continuous independent variable and the number of captures as the dependent variable. The number of captures during the social learning and lure switch phases was compared between anglers using an unpaired, two-tailed Student's *t* test. Angler efficiency (i.e. the ratio of successful captures to the number of strikes felt) was compared between anglers using Fisher's Exact Test.

To determine if pond type (containing trained or naïve demonstrators) impacted catch of observer and demonstrator fish during the social learning phase, two analyses of covariance (ANCOVA) tests were run. The first included the number of observer captures in a given session as the dependent variable, pond type as the fixed factor and session number (1–4) as the covariate. The second test was identical, only with the catch of demonstrator captures as the dependent variable. For each model, the interaction between session number and pond type was tested as well. To determine if observer fish differed from demonstrator fish (regardless of pond type) across angling sessions, a third ANCOVA was run with the number of captures as the dependent variable, fish type (demonstrator or observer) as the fixed factor, session number as a covariate and their interaction as predictor variables. Once again, the interaction between fish type and session number was included in the model.

To determine whether fish are able to generalise their experience with fishing lures to similar and novel lure types, differences in the number of captures throughout all twelve angling sessions (social learning phase and lure switch phase combined) were evaluated using linear regression. For this model, the total number of fish captured across all angling phases combined was set as the dependent variable, and angling session (1–12 for all angling sessions combined) was included as the independent variable. A Chow test was then used to determine if the number of captures significantly changed between the social learning phase and the lure switch phases of the experiment (i.e. between sessions 4–5 and between sessions 8–9). The Chow test examines whether the fit of a regression line through all points can be improved by breaking the regression into multiple sections at pre-determined points, each with its own regression line and parameters (Chow, 1960). The significance of breaks in the overall regression as tested at *a priori* points between sessions 4 and 5 (when the switch to the white plastic worm occurred) and again between sessions 8 and 9 (switch to spinnerbait), which allowed for a determination of whether switching lures significantly impacted vulnerability to capture. While this model is based on linear regression, which may alter overall model fit relative to Poisson regression, the use of a linear model facilitated an examination of whether catch rates changed at particular points using the methodology described. In addition, the risk of overfitting is low in this approach as angling session is the only predictor variable for catch rate, and the

functional breaks were assessed at *a priori* points (rather than examining every possible session for a functional break, which would increase the chance of Type I error). The number of captures for all fish types was pooled for this analysis because observers, naïve demonstrators and trained demonstrators did not differ in their number of captures during the lure switch phase (ANOVA; $F_{1,29} = 0.038$; $p = 0.85$). This indicates that, regardless of whether fish were angled during the social learning phase (naïve demonstrators, observers) or during both the social learning and exposure phases (trained demonstrators), catchability between the fish types had been homogenised prior to the first lure switch.

All analyses were conducted in R version 3.2.1 (R Core Team, Vienna, Austria). Alpha values for significance were set at $p = 0.05$.

3 | RESULTS

Fifty-nine capture events occurred during the exposure phase of angling, with 30 of the available 80 fish captured at least once. The highest number of captures within a day during the exposure phase was recorded in the first session (12), before significantly declining in subsequent sessions, as was expected (Poisson regression, $z = -2.08$, $p = 0.03$).

A total of 495 capture events were recorded across the four angling ponds during the social learning and lure switch phases of angling, from a total of 2,780 angler casts. The number of captures per fish ranged from 0 captures (90 individuals) to 7 captures (1 individual) (Figure 3). Among demonstrators and observers combined, a fish was captured 1.57 times on average, with demonstrators averaging 1.33 ± 0.11 captures and observers averaging 1.82 ± 0.12 captures. Of the 137 fish that were captured multiple times, 78 were caught on the same lure at least twice, while the remaining 59 were caught with a different lure for each recapture. On average, anglers successfully landed fish on 61% of strikes felt, and the proportion of strikes successfully converted into captures did not significantly differ between anglers (Fisher's Exact Test, $p = 0.87$). In addition, anglers did not differ in the mean number of casts attempted over all

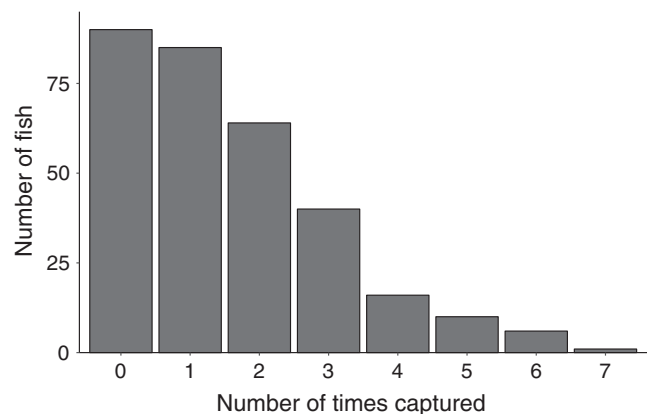


FIGURE 3 The number of largemouth bass that were captured a given number of times during the social learning and lure switch phases of angling

angling sessions (Student's *t* test, $t = -0.21$, $p = 0.83$). As such, data from both anglers were pooled for analysis.

Across all ponds and angling sessions, observer fish were caught significantly more times than demonstrator fish (Table 1). The number of captures for all fish declined with session (Table 1, Figure 3), and the interaction between session and fish type was also significant (Table 1). This interaction was driven by the number of observer captures being very high in session 1 before declining, while the number of demonstrator captures remained relatively constant across the first four sessions (Figure 4). Overall, the total number of captures from the pond types was similar (129 captures in ponds containing naïve demonstrators, 132 captures in ponds containing trained demonstrators).

There was no difference in observer captures between ponds containing trained demonstrators and those containing naïve demonstrators, indicating that observers did not socially learn from trained demonstrators to avoid capture (Table 2). The number of observer captures significantly declined with angling session (Table 2, Figure 4). For demonstrator fish, there was no difference between pond types (i.e. trained and naïve demonstrator fish were equally catchable), and, as stated above, the catch of demonstrator fish did not change with angling session (Table 2, Figure 4).

Across angling sessions 1–12, the number of captures per session for all fish combined declined significantly as sessions progressed (linear regression, $F = 30.89$, $p < 0.001$) (Figure 5). Switching from the green plastic worm to the white plastic worm following session 4 had no effect on number of captures, as capture totals declined consistently across both lure types (Chow Test, $df = 14, 14$, $F = 0.003$, $p = 1.0$). However, changing from the white plastic worm to the spinner bait did have a significant effect on captures (Chow Test; $df = 14, 30$; $F = 10.66$; $p < 0.001$). Specifically, the number of captures in the first session in which the spinner bait was presented (session 9) increased to levels similar to those observed in the first sessions of the social learning phase (Figure 5). In addition, the slope of the regression line between sessions 9–12 was more than twice as steep relative to the slope between sessions 1 and 8 (-5.25 to -2.26), demonstrating that catch rates declined quickly following this initial increase during session 9.

4 | DISCUSSION

While benefits from social learning on non-human predator avoidance have been previously demonstrated (Brown & Laland, 2003),

TABLE 1 Results of an analysis of covariance (ANCOVA) examining the effect of session, fish type (demonstrator or observer) and their interaction on the total number of captures of largemouth bass in a given angling session

Factor	df	F	p
Session	1	4.64	0.03
Fish Type	1	21.21	<0.001
Session*Fish Type	1	5.71	0.02

Note: Significant results are given in bold.

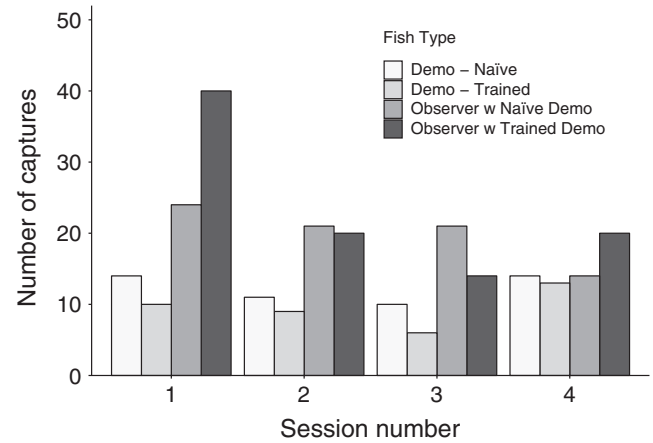


FIGURE 4 Number of fish of each type (naïve demonstrators, observers stocked with naïve demonstrators, observers stocked with trained demonstrators and trained demonstrators) caught during the four social learning angling sessions. Individual bars depict totals across both ponds where each type was present

TABLE 2 Results of two ANCOVA models testing the effects of session, pond type (containing naïve or trained demonstrators) and their interaction on the number of largemouth bass captured during social learning angling sessions

Factor	df	F	p
For Observer Fish Only:			
Session	1	6.45	0.02
Pond Type	1	0.68	0.42
Session*Pond Type	1	0.90	0.35
For Demonstrator Fish Only:			
Session	1	0.06	0.80
Pond Type	1	1.47	0.24
Session*Pond Type	1	0.12	0.73

Note: In the first model, the number of observer fish was set as the dependent variable, and in the second, the number of demonstrator fish was set as the dependent variable. Significant effects are given in bold.

no evidence that naïve largemouth bass were able to learn to avoid angling capture through social interactions with experienced conspecifics was found. Specifically, there was no difference in the catch rates of observers regardless of whether they were in a pond with trained demonstrators (i.e. conspecifics that had experience with angling) or naïve demonstrators (i.e. conspecifics that had never seen a fishing lure). This particular finding relates to indirect learning through the observation of how experienced conspecifics respond to a lure (observational conditioning), and while it does not address the potential for conspecifics to learn to avoid lures through direct observation of conspecifics being captured by a lure, previous work has indicated that this mode of learning may not be a major factor either (Wegener et al., 2018). It was predicted that the presence of conspecifics that had experienced angling would facilitate lure avoidance in angling-naïve largemouth bass through indirect social learning, given how previous studies have found that the presence

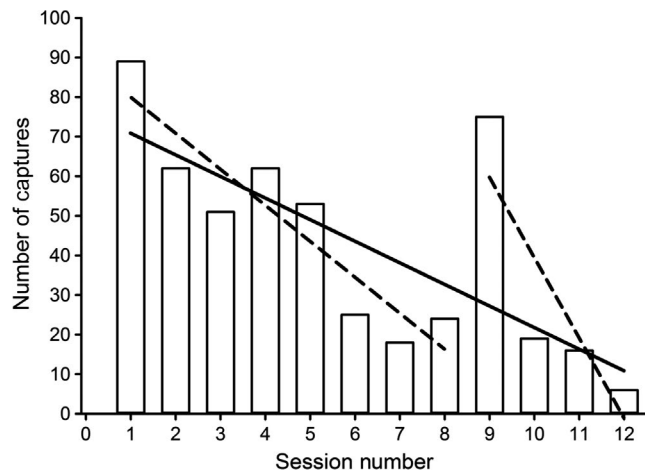


FIGURE 5 Total number of largemouth bass caught in all ponds across all angling sessions, including the social learning phase (1–4) and the lure switch phase (5–12). Sessions 5–8 were fished with a cream-white plastic worm, while sessions 9–12 were fished with a Mepps Agila spinnerbait. The solid line (—) is derived from a linear regression that included all twelve sessions, and the dashed line (- -) represents separate regression lines through sessions 1–8 and 9–12, which improves overall fit as determined by a Chow test

of experienced demonstrators can impact the behaviour of naïve individuals. For example, both zebrafish, *Danio rerio* (Hamilton), and guppies placed into aquaria with conspecifics that were experienced with a simulated trawl net were able to socially learn from experienced individuals to escape capture (Brown & Laland, 2002; Lindeyer & Reader, 2010). Social learning from experienced conspecifics has also facilitated the identification of predator cues in several taxa, including amphibians (Chivers & Ferrari, 2014), birds (Griesser & Suzuki, 2017) and fish (Manassa & McCormick, 2012; Vilhunen et al., 2005). Despite these previous results, no evidence was found that largemouth bass socially learned *via* observational conditioning to avoid fishing lures.

When examining this finding, it is necessary to examine the necessary ingredients for socially learned avoidance to occur. Griffin (2004) described the necessity of a “fear response” on the part of experienced individuals that naïve individuals could detect, and indeed specific anti-predator behaviours (freezing, erratic swimming, the release of alarm cues) on the part of experienced individuals have been found to be key to learning as naïve individuals follow experienced individuals’ lead (Crane & Ferrari, 2016; Crane et al., 2015; Manassa & McCormick, 2012, 2013). This process may not apply to the threat of angling, however, as experienced fish may avoid lures by simply ignoring them, without a pronounced fear response that is detectable by naïve observers. If this is the case, angling-naïve individuals would not be presented with the behavioural cues necessary to identify the lure as a threat. Even if experienced bass were giving off behavioural and/or chemical cues to inexperienced fish, it is possible that the cues were not sufficiently strong to overcome the mal-adaptiveness of avoiding food for inexperienced fish (Beukema, 1970; Garrett, 2002). In addition, it is possible that a lack of social learning could be the result of poor learning performance overall

within this species, as previous work has shown them to be less effective learners compared with other species of fish (Coble, Farabee, & Anderson, 1985). Even if the capacity for social learning is present in largemouth bass, it is also possible that the specific mechanism of social learning at play here (operational conditioning) is something that this species is not able to utilise. This would not, however, preclude largemouth bass from learning socially through other mechanisms, such as by direct observation another individual interacting with a stimulus (Rendell et al., 2011). Finally, it is possible that the lack of lure avoidance on the part of observers was a result of the experimental design, as only 30 of the available trained demonstrator fish were captured (basically, that there weren’t enough lure-experienced demonstrators in each pond). This problem was not an easy one to resolve during the experiment. As mentioned in the results, catch rates of the trained demonstrators during the exposure phase dropped precipitously by the end of the phase, rendering it difficult to establish a population completely composed of fish that had been previously caught. Furthermore, this reason for a lack of difference seems somewhat unlikely given the results themselves, specifically despite there being no significant difference between pond types for observer captures, and the tendency was for the catch of observers to increase in ponds containing trained demonstrators. This suggests a further increase in the number of captured demonstrators likely would not have driven observer captures to levels below those stocked alongside naïve demonstrators. Regardless of the reason for the results, it was concluded that naïve largemouth bass within a population targeted by anglers are not likely to reduce their own catchability by observing how lure-experienced conspecifics interact with lures. This means that, for heavily angled populations, largemouth bass are unlikely to spread knowledge on how to avoid anglers across geographic space very quickly, thus maintaining catchability and angler satisfaction.

Despite, as expected, angling exposure rendering demonstrator fish less vulnerable than observer fish, there were still surprising results with regard to the catch rates of demonstrator fish. Specifically, there was no difference in the number of captures between trained and naïve demonstrators. This result, combined with the lack of difference in observer captures between pond types, caused the total number of captures between pond types to be almost identical (132 total captures in ponds with trained demonstrators, 129 in ponds containing naïve demonstrators). It seems in this case, while experience during the exposure phase did reduce catchability in trained demonstrators (as indicated by observer fish being significantly more catchable than demonstrator fish), lure avoidance learning may have been countered by the effects of increased density following the additional stocking of the naïve observers, resulting in increased vulnerability for trained demonstrators. The suppression of learned behaviour as a result of increased density has indeed been shown in several animal taxa. For example, domestic rats, *Rattus norvegicus*, performed poorly on avoidance tasks after being held in crowded conditions (Goeckner, Greenough, & Mead, 1973). Fish living in high densities experience higher levels of intraspecific competition (Kent, Holzman, & Genin, 2006; Ward, Webster, & Hart, 2006) that may



force individual fish to make quicker decisions to outcompete conspecifics for food (Stoner & Ottmar, 2004), a process that could lead to a greater likelihood of angling capture. With regard to angling, multiple studies have shown that increased density leads to increased vulnerability, for instance in brown trout *Salmo trutta* L. (Harkonen, Hyvarinen, Paappanen, & Vainikka, 2014) and pikeperch *Sander lucioperca* (L.) (Raat, 1991). Furthermore, it has been shown that angled northern pike released into groups were quicker to resume normal foraging activities than those released with no conspecifics present, a finding that presumably would leave these pike more vulnerable to subsequent recapture stemming from their social surroundings (Stålhammar, Linderfalk, Brönmark, Arlinghaus, & Nilsson, 2012). If adding naïve observers created densities high enough to foster intense intraspecific competition, then the effect of learned lure avoidance during the exposure phase on angling vulnerability may have been muted in trained demonstrator fish, resulting in similar numbers of captures with naïve demonstrators. Despite the effect of density-induced intraspecific competition, recognition and avoidance of lures previously encountered still resulted in fewer captures for trained demonstrators compared with the naïve observers they were stocked alongside. This indicates that prior learning as well as the effects of density simultaneously impact the catchability of angled fish.

Results from this study indicate that largemouth bass can utilise prior experience with a fishing lure to avoid a similar lure, but if the lure is highly different, largemouth bass are unable to apply their experience as effectively. This was demonstrated by the catch rates continuing to decline after anglers switched from a green plastic worm to the white plastic worm (i.e. same lure type but different colour), but increased significantly on the first day following a switch to the spinnerbait. Furthermore, there was a difference in the pattern of catchability with the lure types; while the decrease in catch rate with the plastic worms was approximately linear, the catch rate with the spinnerbait plummeted more quickly after spiking in session 9. This could be due to the accumulated effects of angling, with fish becoming quicker to learn after previous experience with other lures, or it could be related to the lures themselves, as previous work found fish learn to avoid larger, more active lures more quickly (Cole, 2014). With regard to the pattern of catch after the lure switches, since all lure switches were conducted in the same sequence in all ponds, it is possible that time itself may have played a role in driving catch rates independent of previous angling experience, but this does not explain the jump in catch rate in session 9 following a continuous decline for the previous 8 sessions. Previous studies have shown that the similarity of a novel stimulus to noxious/dangerous things experienced previously can be a major factor in the decision making of animals. For example, jumping spiders *Phidippus princeps* were found to incorporate visual cues from the potential prey item as well as the environmental surroundings to avoid distasteful prey (Skow & Jakob, 2006). This effect works in the converse as well where new items that are similar to palatable prey are preferred, for instance in predatory blue jays *Cyanocitta cristata*, individuals were more likely to peck at digital images of bugs on a computer screen that were similar to those hunted previously (Bond & Kamil, 2002). If a new

item is not familiar, predators may avoid it, as was seen in both blue jays and in predatory killifish, *Rivulus hartii* (Boulenger), which were unable to recognise guppies initially as prey if the guppies featured an unfamiliar tail coloration (Fraser, Hughes, Tosh, & Rodd, 2013). In the context of angling, Atlantic salmon captured on one gear type are more likely to be subsequently recaptured on a different type, rather than the original gear (Lennox et al., 2016). This particular result indicates an avoidance of the lure type that caused a fish to experience capture, a finding also found in the present study. What remains unanswered from this study is which specific cues fish used to avoid the spinnerbait compared with the plastic worms. While catch rates did not change between worm colours, it remains possible that the red and gold coloration of the spinnerbait may have in, and of, itself elicited more strikes, as has been shown for mackerel, *Scomber japonicas* Houttuyn (Hsieh, Huang, Wu, & Chen, 2001); however, for largemouth bass the role of colour in the attractiveness of a lure has been found to be muted (Moraga, Wilson, & Cooke, 2015). In addition to colour, the spinnerbait and plastic worms differed in several other aspects (texture, vibration given off during retrieve, speed of retrieval), which all could have influenced the vulnerability of fish (Lennox et al., 2017). Furthermore, the different lure types may have not only influenced catch rate for the population, but may have selectively increased the vulnerability of particular individuals as well (Harkonen, Hyvarinen, Niemela, & Vainikka, 2016; Wilson, Brownscombe, Sullivan, Jain-Schlaepfer, & Cooke, 2015). Regardless of what cues are being used, successful avoidance of a potentially noxious or dangerous food source relies in part on previous experience with an item, and its similarity to a new potential food source, a pattern which extends to angling lure avoidance as largemouth bass populations experienced with a lure show reduced catchability when fished with a similar lure, but not one that is different.

While collectively these results can be examined in the context of how animals learn to avoid potential threats, a more specific application can be made in the context of fisheries management. Angler satisfaction within a freshwater fishery is multi-dimensional and can be influenced by a number of factors, including the abundance of large fish, their inherent catchability and other social factors (Arlinghaus, 2006; Arlinghaus, Bork, & Fladung, 2008). The presence of these aspects in a fishery drives economic benefits as more anglers focus their attention on fisheries that they perceive to be valuable or desirable (Beardmore, Hunt, Haider, Dorow, & Arlinghaus, 2015; Hunt et al., 2011). Lure avoidance learning in fish gradually renders fish less catchable over time (Askey et al., 2006; Kuparinen et al., 2010) and is most pronounced in populations that receive high levels of angler effort, leading to a decline in fishery quality even as both the average size of fish and their population levels are maintained (Pierce & Tomcko, 2003; Young & Hayes, 2004). In this study, lure avoidance being learned socially by observing experienced conspecifics was not demonstrated but individuals with prior experience with a lure of similar forms were found to be less likely to be caught. Catchability in this case was impacted by the similarity of a novel lure to previously experienced lures (Bond & Kamil, 2002; Fraser et al., 2013), as largemouth bass



were able to largely avoid capture on a white plastic worm after being previously angled with a green plastic worm, but initially failed to avoid a novel spinnerbait. While Lennox et al. (2016) found that switching from one lure to an unfamiliar lure (artificial flies to either sub-surface lures or live worms) can increase the probability of capturing a fish, this study demonstrates that the effectiveness of lure switching depends on the relative similarity of the new lure to previously experienced lures. For anglers, this means that the use of novel lures may lead to increased catch rates; however, it should be noted that finding adequately novel lures to use may be difficult in heavily fished systems where fish have experienced a host of different lures and presentations (Alós et al., 2015; Kuparinen et al., 2010). In aquatic systems that are not saturated with anglers, this approach may prove more effective. In addition, managers looking to preserve catch rates may recommend that certain lures not be used at particular times of year, in a manner similar to conservation-based approaches to protect heavily exploited species (Herrón, Castellanos-Galindo, Stähler, Díaz & Wolff, 2019; Pérez-Jiménez & Mendez-Loeza, 2015). This type of management may not only preserve catch rates, but may also prevent evolutionary change in fished populations, as it has been demonstrated that different types of lures may selectively and differentially capture fish with particular physiological and u characteristics (Wilson et al., 2015). With regard to how managers inform the public about the health of fish populations, changes in catchability due to avoidance learning may be further augmented by behavioural and trophic responses of fish populations to angling pressure (Matthias, Allen, Ahrens, Beard Jr. & Kerns, 2014; Pine, Martell, Walters & Kitchell, 2009). The end result in many cases is that catch rate is not necessarily indicative of the size of a fish population and can either overestimate (Post et al., 2002) or underestimate (Kuparinen, Alho, Olin, & Lehtonen 2012) fish populations. In the latter case, differences among individual fish in intrinsic vulnerability to angling (Philipp et al., 2009) as well as prior learning (Kuparinen et al., 2010; Young & Hayes, 2004) may cause angler catch rates to be low while populations remain resilient overall. Managers looking to enhance angler satisfaction should therefore advise anglers that lower catchability is not necessarily an indicator of a declining fish population and acknowledge that lure avoidance learning may actually serve as a buffer protecting fish populations from over harvest.

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CONFLICT OF INTEREST

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