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# Quick learning, quick capture: largemouth bass that rapidly learn an association task are more likely to be captured by recreational anglers

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## Abstract
Individuals show consistent differences in their approach to novel tasks (i.e., "cognitive syndromes"), whereby "fast" individuals are bold and solve new problems quickly compared to "slow" individuals. While a "fast" approach can be advantageous in some situations, these individuals are often more likely to make mistakes and subject themselves to greater risk, including from predation. What is unknown is how these tendencies impact survival in environments where humans constitute a predatory risk (such as the case of fish targeted by commercial or recreational fishing). To address this gap, we assessed learning performance in 60 largemouth bass *Micropterus salmoides* using an active-avoidance task that required fish to learn to associate a conditioned stimulus (overhead light) with an unconditioned aversive stimulus (chasing with a net) to successfully shuttle through a small opening to a safe area of an aquarium. These same fish were also tested for proactivity in a restraint test (frequency of leaping to escape a net out of water) before being subjected to angling trials in a naturalistic pond setting. Performance on the active-avoidance task was positively associated with angling vulnerability, as individuals captured by anglers also successfully shuttled on nearly twice as many trials as uncaptured fish. Proactivity was not associated with angling vulnerability or learning performance. These results indicate that a fast cognitive strategy may be maladaptive for fish populations subjected to angling. In addition, because cognitive performance is heritable, fisheries selection based on cognitive traits could cause an evolutionary shift toward slow learning strategies in exploited populations.

## Significance statement
Individual behavioral and cognitive traits can be linked with fitness, especially in human-altered environments. For many freshwater fish, recreational angling by humans poses a major threat, with some individual fish being more vulnerable to capture than others. However, no work has defined whether cognitive traits are linked with an individual's vulnerability. To address this, we conducted a study examining if learning performance is linked to angling vulnerability in largemouth bass, a popular sportfish species. We found that fish that learned to associate a light with a negative stimulus (chasing with a net) and successfully avoid chasing were more likely to be caught in an angling trial. This means that, for targeted species, a fast learning strategy is disadvantageous, and that heavily exploited populations could experience evolutionary shifts toward slower learning speed due to the selective capture of fast-learning individuals.

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# Introduction

Within species, individuals often show consistent differences in their behavioral responses to the environment. These suites of individual characteristics, which are often referred to as "behavioral types" (Bell 2007), "personalities" (Duckworth 2010), or "coping styles" (Koolhaas et al. 1999, 2007), are typically presented as a continuum of behavioral responses to environmental stimuli. Some individuals are described as "proactive" because they exhibit bold and aggressive behavior in response to stimuli, while others are described as "reactive" because they are shyer and more passive (Benus et al. 1991; Overli et al. 2004). These coping styles can be associated with differences in key life history characteristics, whereby proactive individuals display faster growth and greater fecundity (Stamps 2007; Biro and Stamps 2008). Individual differences in behavior emerge in threatening situations, whereby proactive individuals tend toward a "fight or flight" response, while reactive individuals are more likely to freeze and remain immobile until the threat passes (Koolhaas et al. 1999, 2007). An individual's coping style has a major impact on how it responds to environmental change, with reactive individuals typically being more flexible in their behavioral response to environmental shifts (Ruiz-Gomez et al. 2011; Stamps 2016). Particular coping styles, therefore, can be expected to be favored depending on environmental conditions, and, indeed, environmental diversity has been posited as a key factor maintaining a diversity of coping styles within populations (Réale et al. 2010a; Wolf and Weissing 2010).

In addition to differing in behavioral traits, individuals also may differ in cognitive characteristics related to learning and problem solving. Variation in generalized intelligence among individuals has been long described in humans (Deary and Caryl 1997; Duncan et al. 2000), though exactly how to measure intelligence and cognitive performance has long been controversial (Sternberg 2000). In non-human animals, generalized differences in cognitive performance have also been demonstrated where certain individuals consistently perform better on a variety of tasks related to problem solving and learning (Anderson 1993; Matzel and Kolata 2010; Shaw et al. 2015). In recent years, however, a new framework has been posited where performance on cognitive tasks is not based on general intelligence, but rather on the use of alternative approaches to the solving of novel problems. Consistent use of alternative problem solving approaches, termed "cognitive syndromes," are often related within individuals to their coping style (Sih and Del Giudice 2012). Within this framework, "fast" individuals are likely to be proactive behaviorally and are expected to fearlessly approach novel problems and identify solutions quickly. "Slow" individuals, on the other hand, take more time to explore the novel situation, and as such do not arrive at a solution as rapidly. Alternative cognitive syndromes have associated tradeoffs; while fast individuals find solutions to novel tasks quickly, they are more prone to mistakes, less able to commit their experiences to long-term memory, and show a low capacity for changing their behavior based on new information after the initial task has been learned (Sih and Del Giudice 2012). Indeed, the relationship between coping style (i.e., proactive vs. reactive) and cognitive syndrome (i.e., fast vs. slow) has been demonstrated in several animal taxa, including fish (Pintor et al. 2014; Mesquita et al. 2016; Bensky et al. 2017), insects (Udino et al. 2016), birds (Guillette et al. 2009, 2011), and mammals (Guenther et al. 2014; Guenther and Brust 2017) whereby "fast" learning individuals are likely to display characteristics associated with a bold/proactive behavioral phenotype (such as more rapid exploration of novel environments and objects), while "slow" learning individuals are likely to display traits associated with a shy/reactive behavioral phenotype. Depending on the context, these cognitive differences have the potential to greatly impact an individual's fitness (Sih and Del Giudice 2012).

Inter-individual differences in behavior and cognition are especially relevant to fitness in environments altered by human activity. Adequately responding to human-induced threats, whether they be the introduction of invasive species (Mooney and Cleland 2001; Blake and Gabor 2016), harvest (Kuparinen and Merila 2007; Ciuti et al. 2012), or habitat loss (Sih et al. 2016) is essential if individuals are to survive and successfully produce offspring. It is theorized that cognition plays a major role in determining survival in these habitats, with superior cognition being linked to the ability to adjust behavior to both avoid human threats and take advantage of newly presented opportunities (Dridi and Lehmann 2016; Griffin et al. 2017). Independent of cognitive ability, an individual's cognitive syndrome can lead to a tradeoff that influences survival in the face of human activity. On one hand, bold behavior and a fast cognitive strategy may allow individuals to quickly explore human-impacted environments and take advantage of new resources (Sol et al. 2013; Miranda et al. 2013). Conversely, this type of behavior may leave individuals more at risk of mortality as a result of human harvest (Ciuti et al. 2012) or predation by introduced species (Sih et al. 2011). Given that selective mortality of individuals with particular cognitive traits is expected to lead to the evolution of those traits in a population (Sih et al. 2011; Dridi and Lehmann 2016), furthering our understanding of the impacts of cognitive characteristics on survivorship in human-dominated landscapes is essential if we are to make accurate predictions regarding the response of species to environmental change.

A specific example in which cognitive syndromes and learning performance can be linked with survival is in the case of sportfish targeted by recreational fishing. The capacity for learning is well documented in fish, especially with regard to avoiding predators (Chivers and Smith 1995; Manassa and

McCormick 2012, 2013) and identifying profitable foraging patches (Franks and Marshall 2013; Trapp and Bell 2017). This learning ability also extends to learned avoidance of fishing gears, including nets (Brown and Laland 2002) as well as recreational fishing lures (Askey et al. 2006; Lennox et al. 2016). It is also known that individual fish of the same species differ in their capacity for learning (Budaev and Zhuikov 1998), which may lead to differences in overall fitness (Shohet and Watt 2009). In systems targeted by recreational anglers, fitness is likely linked to the ability to successfully avoid striking fishing lures, and, in turn, avoid harvest or incidental mortality from hooking injury. While individual vulnerability to angling has been linked previously to metabolic phenotype (Redpath et al. 2010; Hessenauer et al. 2015), hormonal physiology (Louison et al. 2017), and behavioral type/coping style (Sutter et al. 2012; Harkonen et al. 2014; Klefoth et al. 2017), the relationship between cognitive ability and angling vulnerability has not been examined. This is despite the fact that cognitive ability and individual cognitive syndromes could well be linked to the ability to discern potential danger posed by fishing lures, which would lead to successful lure avoidance. If selective capture of individual fish with certain cognitive characteristics is occurring, it would be expected that exploited populations would then evolve in response away from the traits associated with elevated vulnerability (Arlinghaus et al. 2016; Lennox et al. 2017), potentially leading to cascading effects on the behavior and ecology of targeted populations (Uusi-Heikkila et al. 2008).

To elucidate how cognitive characteristics are linked with vulnerability to capture by anglers, we conducted a study assessing learning performance, proactivity, growth, and angling vulnerability in largemouth bass *Micropterus salmoides*. Largemouth bass are an ideal species for addressing this question, as they are among the most popular sportfish species in North America, have been stocked globally to support recreational fisheries, and have also been a frequent subject for studies examining inter-individual differences in angling vulnerability (Philipp et al. 2009; Redpath et al. 2009). For this study, all fish were first subjected to an active-avoidance protocol (Yue et al. 2004; Morin et al. 2013) to define learning performance, then tested in an out-of-water restraint test to quantify each fish's proactivity. Finally, all fish were stocked into a single naturalistic pond and angled over the course of 10 days, allowing learning performance and proactivity scores to be related to angling capture. We anticipated two alternative outcomes regarding learning performance and angling vulnerability. On one hand, high performance on the learning task would reflect a high level of generalized cognitive ability (Matzel and Kolata 2010; Shaw et al. 2015) that allows individuals to avoid capture. Alternatively, high performance on the learning task would be indicative of a fast cognitive syndrome that would be linked to a higher propensity to be

captured, due to a tendency toward rapid, error-prone exploration of novel lures (Sih and Del Giudice 2012; Guenther and Brust 2017). Under this construct, rapid learning might also be associated with higher levels of proactivity, as assessed in this study by the restraint test (Hau and Goymann 2015; Bensky et al. 2017). Regardless of the outcome, this study quantifies how cognitive performance can influence vulnerability to capture in recreational angling and will allow for novel conclusions regarding the evolution of behavior as a result of selective harvest.

## Methods

### Study fish and holding

Largemouth bass ($N = 60$, mean length ± standard error of the mean = $18.2 \pm 1.5$ cm, range = 16–21 cm) used in this study were acquired from Keystone Fish Hatchery in Richmond, IL on 10 May 2017. All largemouth bass were just over 1 year old at the time of transport and were members of the same hatchery cohort. While on the small end of the range of catchability for this species, this size of fish is expected to be both catchable and large enough to be sexually mature (Nieman et al. 1979; Hessenauer et al. 2016). Upon acquisition, largemouth bass were transported to the Illinois Natural History Survey's (INHS) Aquatic Research Facility in Champaign, Illinois. The INHS facility consists of a wet laboratory as well as a series of naturalistic ponds ranging from 0.04 to 0.12 ha in area, each containing natural macrophyte cover items as well as stocked fathead minnows *Pimephales promelas* that serve as forage for fish. Prior to stocking into one of the 0.12-ha holding ponds, all fish were tagged for individual identification with a 0.8-mm Passive Integrated Transponder tag (PIT; Biomark®, Boise, ID). On 30 May, the holding pond was drained, and the largemouth bass used in the study were retrieved and placed into a series of 1135-L circular outdoor holding tanks at a density of 20 fish per tank. Holding tanks at the facility were designed with continuous flow-through recirculation system that brought a continuous supply of fresh water from a nearby pond into the tanks at a rate of approximately eight full water exchanges per day. During this period, fish were fed daily with commercial pelleted food obtained from Keystone Hatchery, at a daily ration amounting to ~3% of the average fish's body weight. Fish were held in this manner until 10 July, when the first learning assessments took place.

The over-arching goal of this study was to examine relationships between cognitive characteristics and angling vulnerability. Because the cognitive syndromes framework expects that learning performance will relate with behavioral characteristics (Sih and Del Giudice 2012) which are themselves linked with metabolism and growth rate (Stamps 2007),

we also were interested in how growth rate may influence both vulnerability and learning performance. Because all fish used in this study were from the same spawning cohort and identical in age (Keystone Fish Hatchery, personal communication), we considered the length of each fish to be a direct reflection of that fish's growth rate, similar to previous work examining links between behavior and angling vulnerability in hatchery fish (Klefoth et al. 2017).

Behavioral testing for learning performance was done first on the 60 largemouth bass. Assessment for behavior in a restraint test followed; during this test, observers were unaware of each fish's performance in the learning test. Finally, angling trials were conducted in a realistic pond setting, where the angler was again blinded to the results of the behavioral trials (and would be unable to perform any type of biased sampling regardless, given the fact that the fish could not be identified visually during the angling process based on their prior behavioral results).

## Active-avoidance test

To assess learning performance in largemouth bass, an active-avoidance test was conducted using a protocol modified from previously described methods (Budaev and Zhuikov 1998; Yue et al. 2004; Morin et al. 2013). All fish were tested in one of ten 117-L (81 cm long × 40 cm wide × 36 cm high) acrylic aquaria (hereafter, "arenas") connected to a recirculating system that drew water from a common reservoir tank. A TK-500 Heater-Chiller (Teco®, Ravenna, Italy) and a Sweetwater™ air compressor (Pentair, Florida, USA) cycled water within the reservoir tank, and kept water temperatures at 24 °C and dissolved oxygen saturation above 90% in the arenas. Each arena was divided in half along its short axis by an opaque polyethylene sheet that included a 10-cm-diameter circular opening in its center, which allowed for shuttling between the sides of the arena by the fish. Opaque plastic blinds were attached to all sides of the tank to prevent disturbance of the fish by the activity of the observers; however, a small slit was cut into the blinds to allow the observer to determine the location of the fish prior to learning trials.

Successful learning of a task required fish to form an association between a conditioned stimulus and an unconditioned aversive stimulus, in a manner similar to previous assessments (Yue et al. 2004; Morin et al. 2013). To establish this association at the outset of each trial, an observer identified which side of the tank the fish was occupying, and proceeded to shine a light over that side of the tank using a Mag-Lite® LED flashlight for a period of 45 s. The light was then turned off for a period of 15 s, after which the observer manually chased the fish using an aquarium net (15 cm$^2$ cross-sectional area) for a maximum period of 60 s. Chasing of the fish was haphazard in nature in that the net was moved quickly around the half of the arena occupied by the fish in a way that

was not necessarily directed at the fish, and also never restricted the movement of the fish by pinning it against a wall of the arena. Chasing ceased when the fish shuttled through the opening in the divider to the other half of the arena or when 60 s had elapsed. For trials in which shuttling did not occur within 60 s, the observer manually pushed the fish through the opening using the aquarium net. For each trial, three possible outcomes were defined. A trial was considered a "success" when the fish responded to the conditioned stimulus by shuttling through the opening to the other side of the arena prior to the onset of chasing with the net. The trial result was defined as an "escape" when the fish did not shuttle prior to the onset of chasing with the net, but did shuttle before the end of the 60-s chasing period. Finally, the trial was considered a "failure" when the fish failed to shuttle before the end of the chasing period and had to be manually forced through the opening.

Each fish was assessed using this protocol 10 times a day, with 5–10 min between trials, over the course of 3 days for a total of 30 learning trials. The following nine metrics describing learning performance for each individual largemouth bass were then extracted from the outcome data: (1) the total number of successes, (2) the total number of failures, (3) the number of trials until the first escape, (4) the number of trials until the last failure, (5) the number of trials until the first success, (6) the number of trials until the fish succeeded twice consecutively, (7) the number of trials until the fish succeeded three times consecutively, (8) the maximum number of successes within a single day, and (9) the maximum streak of successful trials (including overlaps between testing days). All 60 largemouth bass received active avoidance trials between 10 July and 28 July and were returned to their outdoor holding tank before being subsequently assessed for behavior in a restraint test.

## Restraint test

Following the active-avoidance test, all largemouth bass received a single out-of-water restraint test (Mota Silva et al. 2010; Castanheira et al. 2013), which was chosen because of its possible links to proactive coping styles in fish and its relative ease (compared to laboratory analysis of plasma, for instance). While the repeatability (Bell et al. 2009) of this type of test in fish is unknown, restraint tests which operate on the same principle have proven repeatable in other animal taxa (Burn and D'Eath 2002; Gibbons et al. 2011). Twenty largemouth bass were tested each day over 3 days, beginning on 31 July and ending on 2 August. On the day before each restraint test, 20 fish were each isolated in one half of the behavioral arenas described above, which were modified so that the divider between the halves of the arena included no openings for shuttling. Each largemouth bass was first quickly netted from its holding tank and held out of water in a 30-L plastic container lined with wet towels, where it remained for a

period of 3 min. Three metrics describing the fish's behavior during the restraint test were then described: (1) the total number of jumps, defined as the fish fully displacing its body above the bottom of the container; (2) the time elapsed prior to the fish jumping for the first time; and (3) the time elapsed before the fish jumped for the last time. This restraint test was used as a possible proxy for proactivity in each fish where more proactive fish would be expected to begin jumping earlier, more frequently and for a longer period of time (Mota Silva et al. 2010; Castanheira et al. 2013). Following the conclusion of the restraint test, each fish was returned to the outdoor holding tank.

## Angling trials

On 5 August, all largemouth bass were stocked into a single 0.04-ha angling pond that contained natural cover and stocked forage items as described above. Angling trials consisted of a series of nine daily angling sessions over the course of 10 days, starting on 14 August and ending on 24 August (no angling was performed on 17 August). Each session was 45 min in length, and during that time a single angler (VH) moved around the perimeter of the pond so as to make casts targeting all areas of the pond. Angling gear consisted of a medium-action spinning rod spooled with 2.7 kg Berkely Trilene™ monofilament fishing line. Three different lures were used for this study: a size 0 Mepps® Agila in-line spinnerbait, a Gary Yamamoto® 7.6 cm cream-white plastic worm rigged "wacky style" on a Gamakatsu® Size 6 circle hook, and a third plastic worm setup identical to the previous except that the worm was watermelon green in coloration. Only a single lure was used within each angling session. For the first six sessions, the spinnerbait and white plastic worm were alternated such that the spinnerbait was fished in the first, third, and fifth sessions and the white plastic worm in the second, fourth, and sixth. While the original plan for the study was to alternate these two lures exclusively, we added the third lure (green worm) after these six sessions ended with relatively few captures in order to have a sufficient number of captured fish. The green worm was used in the final three angling sessions. Upon capture, each largemouth bass was dehooked, quickly identified using a hand-held PIT reader, and returned to the pond within 1 min to be potentially re-captured. No largemouth bass were "deep-hooked" in the gills or gullet during the study, and all fish swam away vigorously upon release. Angling trials ended on 23 August, and all 60 fish were recovered when the pond was subsequently drained on 24 August.

## Statistical analysis

To confirm that the active-avoidance test was actually resulting in learning on the part of largemouth bass, we ran two binary logistic regressions that each included trial number as the independent variable. One model included whether the fish succeeded as the dependent variable, and the other included whether the fish failed as respective dependent variables. To account for the fact that the procedure involved repeated testing of the same fish, a random intercept for fish ID was included in each model. A significantly greater likelihood of success as trials proceeded, and a reduced likelihood of failure, would indicate learning on the part of the study population of fish.

After determination that the data were suitable (Kaiser–Meyer–Olkin Test Score = 0.767; Bartlett's Test of Sphericity, $p < 0.001$), principal components analysis based on the correlation matrix was performed to reduce all nine metrics from the active-avoidance test and all three metrics from the restraint test to relevant components. Following this analysis, varimax-rotated components with eigenvalues greater than one were extracted based on the maximum likelihood solution (Kaiser 1960). Within each component, metrics with factor loadings $\geq 0.4$ were considered significant drivers of that component (Kaiser 1960; King et al. 2016). To examine whether growth rate was associated with either learning performance or restraint test behavior, separate linear regressions were used to determine if fish length was associated with extracted components representing learning performance and restraint test behavior.

To determine the relationship between extracted learning performance and restraint test behavior components and angling vulnerability, binary logistic regression was used. For this model, uncaptured fish were coded as a 0, and captured fish were coded as a 1. All extracted components were included as independent variables in the logistic regression model, with capture status as the dependent variable in the model. Because total length correlated positively with one extracted component (see results below), total length was not included in this model to avoid multicollinearity. Student's $t$ tests were also run to directly compare captured and uncaptured fish for all extracted PCs, as well as for total length, and the effect sizes of each variable were additionally assessed using Hedges $g$ (Hedges 1981). We pooled fish regardless of whether they were captured once or twice as only four fish were captured twice (see results below), a sample size too small to examine separately from singly captured fish. In addition, largemouth bass that were captured multiple times did not differ from singly captured fish for any component score or total length (Student's $t$ test, $p > 0.1$ in all cases). All means are shown $\pm$ SE where appropriate, and the level of significance ($\alpha$) for all tests was 0.05. All analyses were performed in R, version 3.4.3 (R Core Team, Vienna, Austria) utilizing the "psych" package (Revelle 2017).

# Results

A summary of means for fish total length and active-avoidance/restraint test metrics for all largemouth bass combined, as well as captured and uncaptured fish separately, are provided in Table 1. On average, it took fish 16.3 trials before succeeding the first time on the active-avoidance test; however, it took only 4.0 trials on average to reach the point where the fish no longer failed (Table 1). Fish ranged between 0 and 67 jump attempts on the restraint test and averaged a total of 38.3 attempts (Table 1).

Largemouth bass showed increased performance on the active-avoidance task as trials were conducted, indicating learning occurred. Specifically, the effect of trial number was significant in predicting whether a fish succeeded ($Z = 8.8$, $N = 241$, $p < 0.001$) and whether a fish failed ($Z = -11.4$, $N = 145$, $p < 0.001$) on the active avoidance test, with fish more likely to succeed and less likely to fail on later trials compared to earlier ones (Fig. 1).

Three extracted principal components describing learning performance and restraint test behavior collectively accounted for 73% of the total variation in the data. The first principal component featured significant negative loadings for the total number of successes, the maximum number of successes within a day, and the maximum streak of successes (Table 2). Significant positive loadings for this component included the number of trials until the first success, the number of trials until two consecutive successes, and the number of trials until three consecutive successes (Table 2). Because more negative scores for this component represented higher levels of success, to facilitate easier interpretation the final "success score" was calculated by multiplying PC 1 scores by $-1$ so that highly positive success scores would represent high-performing learners on the active-avoidance task (this reversed PC score would then be used for all subsequent models). The second principal component featured significant positive loadings for the total number of failures, the number of trials until the first escape, and the number of trials until the last failure (Table 2). This second principal component was interpreted as the "failure score," with higher component scores representing individuals that failed more frequently and took more trials before successfully escaping. The third principal component featured significant positive loadings for the total number of jumps and the time until the last jump was performed, and a significant negative loading for the time taken before the first jump was performed (Table 2). Scores for third principal component were interpreted as the "restraint score" whereby individuals that began jumping sooner jumped more often and longer through the trial received a higher restraint score. The fact that failure-related and success-related metrics were strongly segregated in their loadings among components demonstrates that these two aspects of behavior were not related (i.e., fish with more successes did not necessarily have fewer failures). Furthermore, the segregation of loadings for restraint test metrics on the third principal component shows that behavior on this test was not related to learning performance.

Fish total length was significantly related to success score (linear regression, $t = -2.14$, $r^2 = 0.07$, $df = 1,58$, $p = 0.03$), whereby larger fish succeeded on more trials, took fewer trials to achieve success, and accumulated longer streaks of successful trials in the active avoidance assessment (Fig. 2a). Failure score ($t = 1.18$, $r^2 = 0.02$, $df = 1,58$, $p = 0.24$) and restraint score ($t = 0.9$, $r^2 = 0.01$, $df = 1,58$, $p = 0.37$) were not associated with the total length of largemouth bass (Fig. 2b, c).

Angling trials resulted in the capture of 21 of the 60 fish in the angling pond. Of these 21 fish, four were captured multiple times for a total of 25 total capture events. The green

**Table 1** Summary of means (± SEM) for fish total length and all response variables generated following active-avoidance learning and restraint tests on largemouth bass that were captured or not captured during experimental angling trials

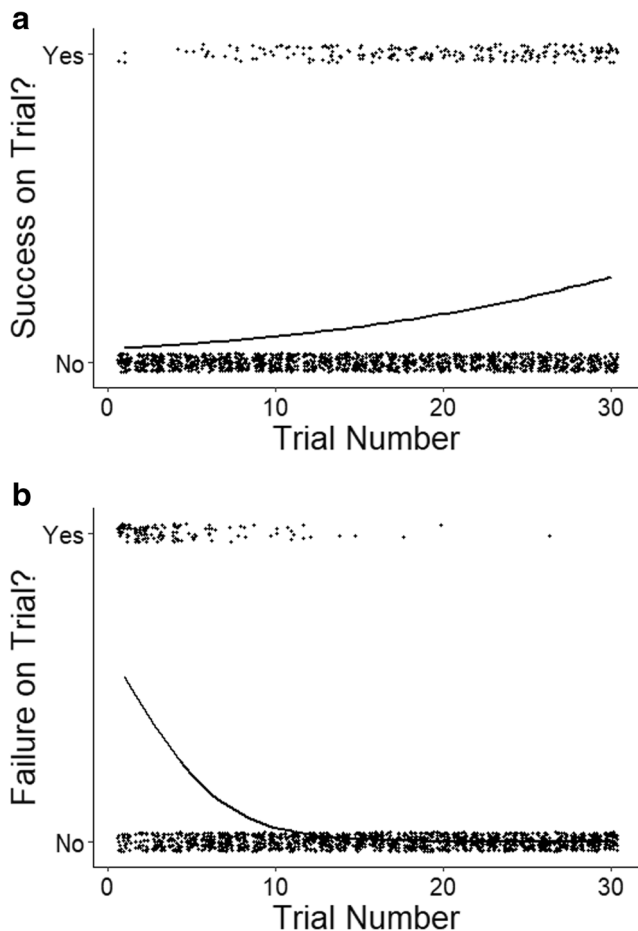| Response variable | Overall (N = 60) | Captured (N = 21) | Uncaptured (N = 39) |
|---|---|---|---|
| Total length (cm) | 18.2 (1.5) | 18.8 (2.4) | 17.9 (1.7) |
| Total failures | 2.3 (0.2) | 2.0 (0.4) | 2.5 (0.3) |
| Total successes | 4.1 (0.5) | 5.7 (0.8) | 3.2 (0.6) |
| Number of trials until first escape | 2.2 (0.2) | 1.9 (0.3) | 2.3 (0.2) |
| Trials until first success | 16.3 (1.3) | 12.6 (1.9) | 18.3 (1.7) |
| Trials until last failure | 4.0 (0.5) | 3.4 (0.7) | 4.3 (0.6) |
| Number of trials until two consecutive successes | 25.3 (0.9) | 22.8 (1.7) | 26.6 (1.0) |
| Number of trials until three consecutive successes | 27.8 (0.6) | 27.5 (0.9) | 28.0 (0.8) |
| Maximum number of successes within a day | 2.6 (0.3) | 3.5 (0.9) | 2.1 (0.4) |
| Maximum streak of successes | 1.9 (0.3) | 2.4 (0.4) | 1.5 (0.3) |
| Time until first jump (s) | 5.5 (3.0) | 10.7 (8.5) | 2.8 (1.4) |
| Total number of jumps | 38.3 (1.7) | 37.4 (3.4) | 38.8 (1.9) |
| Time until the last jump (s) | 141.6 (4.5) | 126.6 (10.2) | 149.6 (3.9) |

**Fig. 1** Performance on the active-avoidance learning task in terms of (**a**) successes and (**b**) failures by $N = 60$ largemouth bass, over the course of 30 individual learning trials. Each dot represents a single trial for a largemouth bass, with the logistic regression line indicating a significant relationship between and whether or not largemouth bass succeeded or failed on the task. Overall, largemouth bass were significantly more likely to succeed and less likely to fail as trials were conducted, indicating learning

plastic worm proved to be the most effective of the three lures used, accounting for 17 of the 25 capture events, while the spinnerbait and white plastic worm accounted for four capture events each.

Higher success scores in the active avoidance test were significantly and positively associated with whether or not a fish was captured (Table 3), with captured fish having a significantly higher active avoidance assessment score (Fig. 3a). The direct comparison between captured and uncaptured fish for success score was also significant (Student's t test, $t = -2.24$, $df = 58$, $p = 0.02$), while captured and uncaptured fish showed no significant difference for failure score ($t = 1.16$, $df = 58$, $p = 0.24$) or restraint score ($t = -0.79$, $df = 58$, $p = 0.42$). Fish length (and by proxy, growth rate) also significantly differed between groups, with captured fish significantly larger than uncaptured fish (Student's t test, $t = -3.23$, $df = 58$, $p = 0.002$). In comparing the effect sizes of the three PCs

as well as fish size on capture status, a large effect of fish length was found (Hedges $g = 0.86$) as was a moderately high effect of success score (Hedges $g = 0.60$). The effect sizes of failure score (Hedges $g = 0.31$) and restraint score (Hedges $g = 0.06$) were small by comparison. The number of trials in which a fish failed on the avoidance assessment, as well as the fish's behavior during the restraint test, were not significantly associated with capture (Fig. 3b, c, Table 3).

## Discussion

Results from this study demonstrate a link between learning performance and angling vulnerability in a highly sought-after sportfish species in that largemouth bass that performed better on the active-avoidance task were more likely to be captured during experimental angling trials. The principal component representing success score was loaded most heavily by the number of successful trials in the active-avoidance test, and captured fish successfully shuttled in response to the light more often than uncaptured fish. In addition to achieving more successes, captured fish required approximately six fewer trials on average to achieve their first success than uncaptured fish. Given the nature of the test administered, it is possible that the link between low performance and low angling vulnerability could reflect a propensity to freeze in response to threats (Koolhaas et al. 1999) in some fish, a tendency that would cause them to both be slower to escape and slower to strike a lure, a link that has been proposed previously (Louison et al. 2017; Koeck et al. 2018). Alternatively, behavior in the active-avoidance task could be reflective of an individual's cognitive approach to a novel challenge, with faster learners being more vulnerable to capture. While the fact that better learners were less adept at avoiding fishing lures may seem counterintuitive, this result is consistent with the predictions drawn from research examining cognitive syndromes. Within the cognitive syndrome framework, individuals that employ a fast learning strategy are quicker to initially learn a task (especially tasks based on movement and activity, such as the protocol used in the present study), while those employing a slow strategy may take longer to initially learn a task, but are superior at retaining that information and adapting to new information and environmental cues (Guillette et al. 2011; Sih and Del Giudice 2012; Guenther et al. 2014). Fast learning strategies have also been linked to an individual's behavioral characteristics, with proactive and bold behavior linked to initial learning speed in several animal taxa, including birds (Guillette et al. 2009), mammals (Guenther et al. 2014; Guenther and Brust 2017), and fish (DePasquale et al. 2014; Mesquita et al. 2016; Bensky et al. 2017). This rapid learning and bold behavior comes at a potential cost, as individuals with these traits have been found to be more prone to mistakes (Sih and Del Giudice 2012), and also more vulnerable to

**Table 2** Principal component loadings for all metrics derived from assessments for learning and restraint test performance in largemouth bass

| Response variable | PC1 (success score) | PC2 (failure score) | PC3 (restraint score) |
|---|---|---|---|
| Total successes | **− 0.96** | − 0.14 | 0.00 |
| First success | **0.71** | 0.30 | 0.17 |
| Number of trials until two consecutive successes | **0.85** | 0.06 | 0.11 |
| Number of trials until three consecutive successes | **0.83** | − 0.10 | 0.01 |
| Maximum number of successes within a day | **− 0.96** | − 0.04 | 0.01 |
| Maximum streak of successes | **− 0.90** | − 0.01 | 0.02 |
| Total failures | 0.08 | **0.95** | 0.07 |
| Number of trials until first escape | − 0.04 | **0.68** | − 0.18 |
| Last failure | 0.16 | **0.81** | 0.18 |
| Time until first jump | 0.14 | 0.08 | **− 0.79** |
| Total number of jumps | 0.14 | 0.07 | **0.76** |
| Time until the last jump | 0.11 | 0.05 | **0.81** |
| Total variance explained | 39% | 18% | 16% |
| Eigenvalue | 4.8 | 2.1 | 1.8 |

All learning metrics are based on the outcome (success, escape, or failure) of 30 active-avoidance trials for each individual fish. Restraint test performance was based on how often and for how long a fish continued to "jump" while being held in a container out of water over 3 min. Three principal components were extracted and subsequently named based on the factors which loaded most heavily on each component (significant loadings ≥ 0.4 are given in bold)

predation while actively foraging (Sih et al. 2003, 2004; Stamps 2007). Within the context of cognitive syndromes, striking a fishing lure may constitute a major "mistake," which "fast" individuals (which tend to approach novel stimuli quickly without fully inspecting them) may find themselves more prone to (Sih and Del Giudice 2012). Indeed, recreational harvest of fish species represents a major predation risk, and, several studies have shown that individuals that are bolder, more active, and/or more exploratory are more vulnerable to hook-and-line angling as a result of their tendency to actively explore novel lures and strike (Harkonen et al. 2014; Alós et al. 2016; Klefoth et al. 2017; present study), though this finding has not been unanimous (Wilson et al. 2011; Louison et al. 2017). The present study shows that, in addition to behavioral phenotype, cognitive learning style also drives angling vulnerability, as "fast" individuals that perform an active-avoidance task more quickly are also more likely to investigate and strike a novel fishing lure.

In addition to being linked with vulnerability to angling, learning performance was also associated with fish size. Success score was significantly and positively related to fish length, while failure score and restraint score were not. While the relationship between success score and fish length was indeed significant, the overall degree of variance in behavior explained by length was not overly high ($r^2 = 0.07$), likely reflecting the large amount of variation in the behavioral data that had to be explained by a rather small amount of variation in fish size (~ 5 cm range between the largest and smallest fish). As all largemouth bass in this study were acquired from

a hatchery and were from the same age cohort, larger fish were almost certainly faster growers within the cohort, meaning that a positive relationship between learning performance and growth rate can therefore be inferred. From an angling perspective, while a fished population will undoubtedly contain older large individuals that are slow growers, fast growth is still likely to be a driver of angling vulnerability as fast growers reach a catchable size more quickly (Biro and Post 2008). Faster growth has been shown to be correlated with fast and proactive behavioral and physiological characteristics (Stamps 2007; Biro and Stamps 2008, 2010). This fast "pace of life" (Réale et al. 2010b) has recently been linked to fast cognitive syndromes and rapid initial learning (Sih and Del Giudice 2012). These characteristics are associated with a tradeoff that incurs higher mortality risk (Stamps 2007), a relationship that holds in the present study where fast cognitive syndrome/fast-growing largemouth bass were more vulnerable to angling. Indeed, selection based on correlated growth and behavioral characteristics has been described previously in both fish (Biro and Post 2008) and commercially harvested crustaceans (Biro and Sampson 2015). From a mechanistic standpoint, either behavior or growth rate could be the primary driver of vulnerability in fish. On one hand, fish that make rapid decisions and exhibit bold behavior may be more likely to approach and strike a fishing lure (Klefoth et al. 2013). Alternatively, vulnerability could be driven by growth rate via differences in mouth size, with larger-mouthed fish being better able to take the lure into their mouth while smaller fish fail to fully take in the lure, increasing the
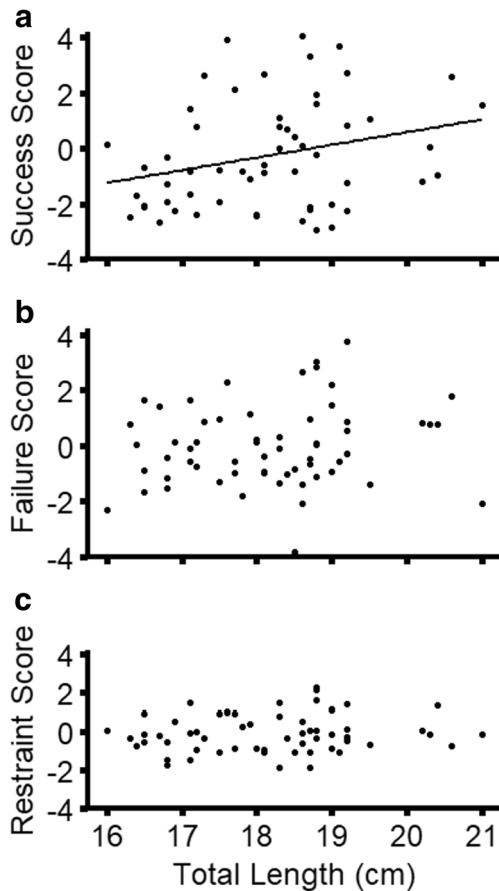
**Fig. 2** Relationships between total length (cm) and (**a**) success score, (**b**) failure score, and (**c**) restraint score across largemouth bass assessed for learning performance in an active-avoidance learning test and proactivity in a restraint test ($N = 60$). Analyses performed to generate the three different response variables are outlined in Table 2. The regression line in (**a**) indicates a significant positive relationship between largemouth bass length and success score, as determined by simple linear regression. Relationships between total length and both failure score and restraint score were not significant

**Table 3** Output from binary logistic regression model (McFadden $R^2 = 0.09$) analyzing the relationship between extracted components following a learning trial and a restraint test (success score, failure score, restraint score) and angling capture in largemouth bass

| Term | Estimate | SE | Z score | p value |
|------|----------|-----|---------|---------|
| Intercept | **− 0.69** | **0.29** | **− 2.36** | **0.01** |
| Success score | **0.29** | **0.13** | **2.15** | **0.03** |
| Failure score | −0.25 | 0.20 | −1.22 | 0.22 |
| Restraint score | 0.15 | 0.22 | 0.72 | 0.47 |

Significant effects are given in bold

chances of successful hooking and landing by the angler (Alós et al. 2014; Klefoth et al. 2017). These first two mechanisms could provide a rationale for the present results whereby the relationship between learning performance and angling vulnerability is necessitated by size (i.e., size is the major factor, not learning performance per se), but the behaviors associated with a fast cognitive strategy drive greater foraging and faster growth, leading to being recruited to catchable size more quickly. Indeed, $t$ tests comparing captured and uncaptured fish found a far stronger level of significance for total length ($p = 0.002$) than for success score ($p = 0.02$), as well as a stronger overall effect size (Hedges $g = 0.86$ for total length and 0.60 for success score). This possibly indicates that, for this age class of largemouth bass, the behaviors under angling selection will necessarily be those linked with faster growth, which is the primary driver of vulnerability. Whether or not one of these mechanisms (or both) is driving the relationship between size and angling vulnerability, it can therefore be

expected that fisheries selection in heavily fished ecosystems will affect both cognitive behavior and growth rate simultaneously.

In contrast to learning performance, behavior in a restraint test was not associated with angling vulnerability in largemouth bass. In addition, measures of behavior derived from the restraint test (number of jumps, the time until the first and last jump) did not load on either of the learning performance components, indicating that learning and "proactivity" as defined in this assessment are likely not related. This finding contrasts with previous studies demonstrating links between proactive behavioral traits and a fast cognitive syndrome (Sih and Del Giudice 2012). Several proactive behavioral and physiological traits have been found to be positively linked with angling vulnerability in fish, including low hormonal responsiveness to stress (Louison et al. 2017; Koeck et al. 2018), high metabolic rates (Redpath et al. 2010), and boldness in a behavioral assay (Harkonen et al. 2014; Klefoth et al. 2017). On one hand, it is possible that proactivity as a driver of angling vulnerability does not establish itself until fish are of a larger size, as the fish in this study were 1+ years and were on the small end of the catchable range for this species. Alternatively, it should be noted that the restraint test used in this study is only one measurement of proactivity and that different assessments for proactivity do not always align with each other (Backstrom et al. 2014; Boulton et al. 2015). Given this, our measure of proactivity (restraint test) may not have been reflective of other aspects of proactivity that are predictive of angling. In describing how different behavioral traits may link with each other along the proactive–reactive axis, Koolhaas et al. (2007) described the behavioral response to environmental stimuli in terms of both "proactivity" and "emotionality," which describe both the approach an individual takes to a stimulus as well as the magnitude of the behavioral response, respectively. In the present study, largemouth bass differed in their behavioral responses during the restraint test; however, these differences do not necessarily align with other measures typically used to measure proactivity, such as boldness and cortisol responsiveness, which may reflect other components of the individual's coping style (Koolhaas et al. 2007). Indeed,
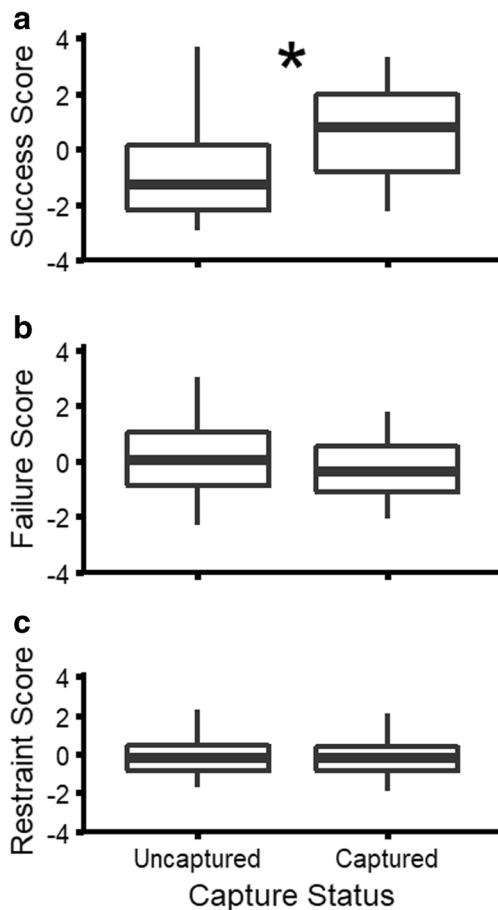
**Fig. 3** Boxplots showing comparisons between largemouth bass that were either captured or not captured during experimental angling trials and (**a**) success score, (**b**) failure score, and (**c**) proactivity score. Analyses performed to generate the three different response variables are outlined in Table 2. The asterisk (*) in (**a**) indicates a significant difference between captured and uncaptured fish for success score, as determined by binary logistic regression. Boxes show the median and interquartile range, while whiskers extend to the lowest and highest point up to 1.5 times the interquartile range

demonstrated in both marine (Conover et al. 2009; Hidalgo et al. 2014) and freshwater (Consuegra et al. 2005; Edeline et al. 2007; Philipp et al. 2009) fish species. While life-history characteristics relevant to commercial harvest have been oft-studied (Jorgensen et al. 2007; Kuparinen and Merilä 2007; Enberg et al. 2010), the potential for selection based on individual behavioral phenotype to evolutionarily disrupt fish behavior has been quantified as well (Sutter et al. 2012; Harkonen et al. 2014; Arlinghaus et al. 2016). Cognitive abilities have been demonstrated to be heritable in fish (Smith et al. 2015) and based on the results of the current study, cognitive learning characteristics may be under selective pressure in exploited populations, with slow learners having an evolutionary advantage through reduced capture. We would expect, therefore, a population-level reduction in the speed of learning that could impact behaviors such as foraging and habitat selection that require associative learning. However, given the current lack of empirical findings regarding the role of cognitive traits in driving angling vulnerability in wild populations, relating the present findings to wild populations is somewhat tenuous. Selection favoring a slow cognitive strategy may actually be beneficial in wild populations, particularly in rapidly changing environments where slow explorers/ learners have been shown to be more flexible when environmental change occurs (Koolhaas et al. 1987; Ruiz-Gomez et al. 2011). Indeed, while the present study is related specifically to angling vulnerability in fish, human-caused selective mortality favoring flexible phenotypes has been predicted to be beneficial in a variety of additional contexts, such as in the face of habitat destruction or the introduction of predatory invasive species (Sih 2013). This means that, for taxa where human activity leads to selective mortality, we would expect that individuals with flexible behavior and a "slow" cognitive syndrome would be evolutionarily favored.

## Conclusion

Recent work has demonstrated the existence of cognitive syndromes, whereby individuals consistently differ in their learning performance and approach to novel problems (Sih and Del Giudice 2012; Guenther and Brust 2017). These differences are often described in terms of a continuum, where fast individuals show greater speed in initially learning activity-based tasks, while slow individuals show greater flexibility and investigate new tasks with a higher degree of thoroughness. In the present study, individuals that performed better on an avoidance task were also more likely to be captured by anglers. This finding is, to our knowledge, the first to demonstrate that cognitive characteristics in fish may be under selective pressure due to human activity, specifically intensive fishing pressure. In environments altered by humans, it has been suggested that individuals that show greater flexibility and

while Louison et al. (2017) found that largemouth bass that showed a low cortisol response to air exposure were more likely to be captured, boldness in a behavioral assay was not related to angling vulnerability, indicating that these two components typically associated with proactivity may not linked. Collectively, this means that a fish's response during a restraint test may not be reflective of other aspects of proactivity, and that additional proactive behavioral characteristics such as cortisol responsiveness or behavior under risk are better linked with learning performance, and thus angling vulnerability.

The potential for selective capture of individual fish based on their cognitive, behavioral, or physiological characteristics is of interest to behavioral scientists and fisheries researchers alike, due to the evolutionary consequences of such selection. Fisheries-induced evolution has been predicted by numerous modeling approaches (Kuparinen and Hutchings 2012; Eikeset et al. 2013; Dunlop et al. 2015), and empirically

lower activity may have an advantage in terms of avoiding conflict with people (Ciuti et al. 2012; Sih 2013). Because these traits are often associated with a slow cognitive approach, the present results reinforce this concept as slow-learning largemouth bass were better able to avoid capture. Whether human-induced selection based on this characteristic is widespread in nature, or applies to multiple targeted species, is still unknown. Additional research involving multiple taxa impacted by human activity will be needed to determine how cognitive characteristics impart fitness advantages or disadvantages in disturbed environments.

## Compliance with ethical standards

**Ethical statement** This work was supported by Federal Aid in Sport Fish Restoration Project via the United States Fish and Wildlife Service, project F-69-R to J.A.S. All experimental procedures were approved by and conducted in accordance with the University of Illinois Institutional Animal Care and Use Committee (IACUC), protocol no. 17065. 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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