

Behavioral phenotype does not predict habitat occupancy or angling capture of largemouth bass (*Micropterus salmoides*)

T.D. Keiling, M.J. Louison, and C.D. Suski

Abstract: Fish behavior types can predict angling vulnerability, providing insights about how recreational fishing may lead to artificial trait selection. Most vulnerability studies have focused on species with active foraging strategies, and the impact of environmental conditions on vulnerability has not been quantified. The objective of this study was to determine the influences of behavior types and habitat on angling vulnerability of largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) — a sit-and-wait predator. Behavior assays quantified individual activity and boldness, then experimental angling took place in ponds with two habitat treatments: (1) structured habitat with artificial structures present and (2) open habitat with no structures added. Two anglers determined which individual largemouth bass were vulnerable to capture across the two contexts. In contrast with previous studies involving active foragers, behavior types of largemouth bass did not influence capture, regardless of habitat type. The number of captures also did not differ between structured and open habitat. However, anglers captured fish with different behavioral phenotypes, revealing additional complexity for factors that may affect behavioral selection. Findings suggest that angling may not be selecting for specific activity or boldness phenotypes of largemouth bass, even across habitat types, but that anglers may influence selection.

Key words: artificial selection, behavioral syndrome, fisheries-induced evolution, largemouth bass, *Micropterus salmoides*, personality, temperament.

Résumé : Les types de comportements des poissons peuvent permettre de prédire la vulnérabilité à la pêche sportive à la ligne, fournissant ainsi de l'information sur une possible sélection artificielle de caractères découlant de la pêche sportive. La plupart des études de la vulnérabilité se sont intéressées à des espèces présentant des stratégies actives de quête de nourriture, et l'incidence des conditions ambiantes sur la vulnérabilité n'a pas été quantifiée. L'objectif de la présente étude était de déterminer les influences des types de comportements et de l'habitat sur la vulnérabilité à la pêche à la ligne des achigans à grande bouche (*Micropterus salmoides* (Lacepède, 1802)), un prédateur qui reste immobile en attente de ses proies. Des tests comportementaux ont quantifié l'activité et la témérité d'individus, puis une pêche expérimentale à la ligne a été effectuée dans des étangs présentant deux traitements d'habitat, soit (1) un habitat structuré présentant des structures artificielles et (2) un habitat ouvert sans structures ajoutées. Deux pêcheurs ont déterminé quels achigans à grande bouche étaient vulnérables à la prise dans les deux contextes. Contrairement aux études antérieures portant sur des espèces empruntant des stratégies actives de quête de nourriture, les types de comportements des achigans à grande bouche n'avaient pas d'influence sur la prise, quel que soit le type d'habitat. Le nombre de prises ne différait pas non plus entre l'habitat structuré et l'habitat ouvert. Les pêcheurs ont toutefois pris des poissons présentant différents phénotypes comportementaux, révélant ainsi une complexité supplémentaire en ce qui concerne des facteurs pouvant avoir une incidence sur la sélection de comportements. Les constatations donnent à penser que la pêche sportive à la ligne pourrait ne pas sélectionner de phénotypes particuliers d'achigans à grande bouche en matière d'activité ou de témérité, même dans différents types d'habitats, mais que les pêcheurs pourraient avoir une influence sur la sélection. [Traduit par la Rédaction]

Mots-clés : sélection artificielle, syndrome comportemental, évolution induite par la pêche, achigan à grande bouche, *Micropterus salmoides*, personnalité, tempérament.

Introduction

Habitat quality is a key element aiding the survival of all fish. As a result of its importance, fisheries managers allocate millions of dollars to restore fish habitats with the expectation of increased fish abundances, carrying capacities, and survival (Baumann et al. 2016; Roni 2019). Often, management goals for habitat restoration also include societal factors, such as increases in angler satisfaction, which can be achieved through increased catch rates (Bolding et al. 2004; Smokorowski and Pratt 2007). Habitat conser-

vation and restoration are therefore important for the stability of fish populations and to enhance recreational angling.

Although increased fish capture by recreational anglers can result in increased satisfaction, it can also increase negative impacts on fish populations through human-induced evolution. For example, anglers can negatively influence fish populations through the disproportionate capture and harvest of fish with suites of correlated, repeatable traits, including bold or active behavioral phenotypes and fast growth (i.e., “fast” life history), commonly referred to as fisheries-induced evolution (FIE) (Heino

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T.D. Keiling, M.J. Louison,* and C.D. Suski. Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA.

Corresponding author: T.D. Keiling (email: toniannkeiling@outlook.com).

*Present address: McKendree University, Lebanon, IL 62254, USA.

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et al. 2013). More specifically, should anglers disproportionately harvest fish with “fast” life-history traits, this can lead to the predominance of timid individuals in a population that are less likely to encounter, approach, inspect, and strike fishing lures (referred to as the timidity syndrome), possibly leading to declines in catch rates and angler satisfaction (Arlinghaus et al. 2017b). Selection of “fast” life-history individuals through FIE can also extend to other correlated traits, leading to selection against high metabolic rates and fast reproduction (Reale et al. 2010). Through the removal of certain traits, FIE can reduce genetic and behavioral phenotypic diversity of a stock and threaten population stability much faster than through natural selection in as short as a few generations (Reznick and Ghalambor 2001; Laugen et al. 2014; Uusi-Heikkilä et al. 2015). Selective fishing pressure can lead to negative effects for fish populations, from genetic to ecological scales.

Individual behaviors, however, are not always repeatable across environmental contexts, and fish may adjust behavioral flexibility to benefit from current conditions (Mittelbach et al. 2014; Mazué et al. 2015). For example, work by Savino and Stein (1982) demonstrated that largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) alter foraging strategy based on habitat complexity, with fish showing more active foraging strategies in habitats with low complexity and shifting to sit-and-wait foraging strategies as structural complexity increases. Similarly, Ehlinger (1989) showed that bluegill (*Lepomis macrochirus* Rafinesque, 1819) learned to forage at high speeds in open habitat, but at slower speeds in more vegetated habitats, to maximize foraging efficiency. Additionally, behavioral traits have been linked to habitat use by fish, with timid fish more likely to associate with shelter compared with bold conspecifics (Hollins et al. 2018). These changes in microhabitat use have the potential to influence the capture of fish across habitat types. For example, as seen in a study with Eurasian perch (*Perca fluviatilis* Linnaeus, 1758), food shortage during the autumn months led to increased foraging behavior to meet energetic demands, decreased body condition, and increased capture rates; the latter of which was most likely influenced by increased encounters with fishing lures and lure-striking behaviors as fish foraged more vigorously (Heermann et al. 2013). Thus, fish behaviors can co-vary with altered environments, including changes in habitat, and behavior can also be influenced by personality, which in turn can influence foraging and capture by anglers.

Despite our understanding of behavioral flexibility, as well as the role that behavior can play in influencing capture by anglers, it is still unknown how behavior type and angling vulnerability interact across habitat types, or if this interaction of behavior type and habitat can help define how anglers can influence the evolution of fish populations. Therefore, the objective of this study was to quantify the combined influence of behavioral phenotype and habitat preference on angling vulnerability in largemouth bass. Previous work has shown that largemouth bass typically reside in littoral areas, rarely making large-scale movements (Demers et al. 1996), employing a sit-and-wait strategy to ambush prey, particularly in structurally complex habitats (Savino and Stein 1982; Ahrenstorff et al. 2009), and will display reduced growth rates in environments with low littoral habitat complexity (Schindler et al. 2000; Sass et al. 2006). To accomplish this objective, we designed a combination laboratory- and pond-based study that first quantified activity and boldness behaviors in largemouth bass and then subjected these fish to experimental angling in ponds within open habitat and structured habitat. Based on previous work on angling vulnerability (Laugen et al. 2014; Uusi-Heikkilä et al. 2015; Arlinghaus et al. 2017b), we predicted that “bold” largemouth bass would be disproportionately captured in open habitats, whereas “shy” individuals would be preferentially captured in areas with supplemental structure; we also predicted that fewer “shy” individuals would be captured relative to the number of “bold” individuals.

Materials and methods

Study animals

Largemouth bass ($n = 250$) were acquired from Seven Springs Fish Farm, Evansville, Illinois, USA, and transported to Illinois Natural History Survey Aquatic Research Facility near Champaign, Illinois, USA, on 16 May 2018. This fish hatchery has been raising largemouth bass in their facility for multiple generations and all largemouth bass were pellet-reared. Mean (\pm SD) total length of fish was 281 ± 20.9 mm, mean (\pm SD) mass was 313 ± 90.0 g, and mean (\pm SD) relative weight was 96.3 ± 7.8 , based on standard mass calculations for largemouth bass (Murphy et al. 1991). Relative weight is a metric that illustrates how plump a fish is for its length and is therefore used to determine individual condition. This metric is often paired with other information, such as relative abundance and size structure, to describe the status of sportfish populations (Murphy et al. 1991). This size of largemouth bass has previously been shown to be vulnerable to angling in both laboratory simulation studies and in wild populations (Murphy et al. 1991; Hessenauer et al. 2016; Sass et al. 2018). Once at the Research Facility, all largemouth bass were divided among 12 circular 1135 L outdoor tanks supplied with continuous flow-through, aerated water from an adjacent 0.04 ha earthen pond at a rate of ~ 8 water exchanges per day. Mean (\pm SD) water temperature was 26 ± 2.1 °C and mean (\pm SD) dissolved oxygen concentration was 8.6 ± 0.9 mg/L (Professional Plus dissolved oxygen and temperature meter; YSI Inc., Yellow Springs, Ohio, USA) during holding. Fish were fed Skretting (Tooele, Utah, USA) high protein pellets ad libitum daily. All fish were implanted with a passive integrated transponder (PIT) tag (10 mm length \times 2 mm diameter; HPT12 PIT tag; Biomark Inc., Boise, Idaho, USA) for individual identification 3 days after transport. Following tagging, fish acclimated to holding conditions for an additional 6 days before behavior assays began on 25 May 2018.

Behavior assays

One hundred thirty-two largemouth bass were haphazardly selected to complete behavior assays. For these assays, fish were first moved from outdoor tanks to indoor aquaria to acclimate to laboratory conditions for between the hours of 1700 and 2300 prior to assessments. Indoor aquaria (121 L opaque plastic holding tanks) were each divided into two chambers by an opaque plastic barrier with holes to allow for water flow between the chambers. Each aquarium held two fish, one on either side of the barrier. A reservoir tank, equipped with an aerator, provided a re-circulating supply of water to all aquaria through a pump (Outdoor air pump; Pentair, Cary, North Carolina, USA). Indoor aquaria temperature was maintained at 23.8 ± 0.7 °C with a TK 500 Heater-Chiller (Teco, Revenna, Italy) and dissolved oxygen concentrations remained above 7.51 ± 0.5 mg/L, verified daily with a hand-held probe (YSI Inc. Professional Plus, Yellow Springs, Ohio, USA).

Behavior assays were conducted between the hours of 0830 and 1430, from 25 May 2017 to 7 June 2017, in one of two identical arenas. Arenas were opaque 94 L circular tanks (80 cm diameter) filled to a water depth of 24.5 cm with water from a nearby pond. Video cameras (GoPro Hero 3 or Session 4; GoPro, San Mateo, California, USA) suspended above the arenas from a frame made from polyvinyl chloride (PVC) pipes were used to record fish location and behavior. The arena consisted of two zones: a refuge zone and an open zone. The refuge zone occupied the perimeter of the tank and had a natural gravel bottom with plastic aquarium plants for shelter; the open zone occupied the center of the tank and had no gravel substrate or vegetation. Each refuge zone had eight evenly spaced aquarium plants, each about 17 mm tall and 8 mm wide, made up of several separate leaf blades, with the bottom of the plant anchored into the gravel bottom. The open zone was 40 cm in diameter and the refuge zone had a radius of 20 cm when measured from the tank perimeter to the outside of

the open zone. The behavioral arena was similar to others used to measure habitat preference (Hart et al. 2009).

For the behavior assay, largemouth bass were netted from the indoor aquaria, identified to individual using a PIT-tag reader, and placed into the center of the open zone of an arena. Fish were left to acclimate for 10 min immediately before behavior assays commenced, during which time movement was unrestricted and fish could move freely around the arena. A 10 min acclimation time is common for behavior assays (Vainikka et al. 2016; Louison et al. 2017), and preliminary trials revealed that fish began moving around the arena typically within 5–6 min after the transfer. Video cameras recorded behavior for a 10 min period following the acclimation period to collect baseline data.

Following this generation of baseline data, fish were subjected to a simulated predator attack. For this attack, a Great Blue Heron (*Ardea herodias* Linnaeus, 1758) model measuring 73.7 cm in height was used (United Aquatics LLC, Marlton, New Jersey, USA), as Great Blue Herons are a common largemouth bass predator and have been used as predator models in other fish behavior studies (Cooke et al. 2003; Bell and Stamps 2004). The simulated predator attack involved an observer that held the heron model over the behavioral arena and struck the water four times in a square pattern in the center of the open zone with the heron's beak. The heron strike locations were the same across trials and did not vary with the fish's position in the arena. Fish behavior was then monitored for 10 min after conclusion of the simulated predator attack, following which behavior assays were considered to be complete and video recording ended. Largemouth bass were then returned to the indoor aquaria where they were left for 7 days.

After this 7 day period, the entire behavioral assay was conducted a second time in its entirety for all fish, and this second test allowed for the calculation of repeatability metrics for the measured behaviors (Bell 2007). Following this second behavioral assay, largemouth bass were again returned to the outdoor tank system.

Five metrics were used to score fish behavior observed during the behavior assay: (1) time spent swimming (s) before the simulated predator attack (termed pre-predator swimming activity), (2) time spent in the open zone (s) before the simulated predator attack (termed pre-predator open zone), (3) duration of the freeze response (s) after the simulated predator attack (termed freeze time), (4) time spent swimming (s) after the simulated predator attack (termed post-predator swimming activity), and (5) time spent in the open zone (s) after the simulated predator attack (termed post-predator open zone). A fish was considered to be swimming when horizontal displacement in the water column was observed. Time spent in the open zone was recorded if more than half of the fish's body length was within the open zone boundary. Freeze time was the recorded time (s) between when the fish initiated the freeze response after the simulated predator attack until the fish resumed movement; a movement was deemed to occur when the fish completed a half body length displacement, or performed a lateral turn of approximately 90°. Time spent swimming was a metric of activity, whereas freeze time and time spent in the open zone of the tank were boldness behaviors (Réale et al. 2007). Two boldness measures were used because different boldness metrics may be uncorrelated, and multiple metrics should be generated to adequately describe behavioral types (White et al. 2013). Durations of all performed behaviors were recorded using Solomon Coder version beta 17.03.22 (available from <https://solomon.andraspeter.com/>).

Angling trials

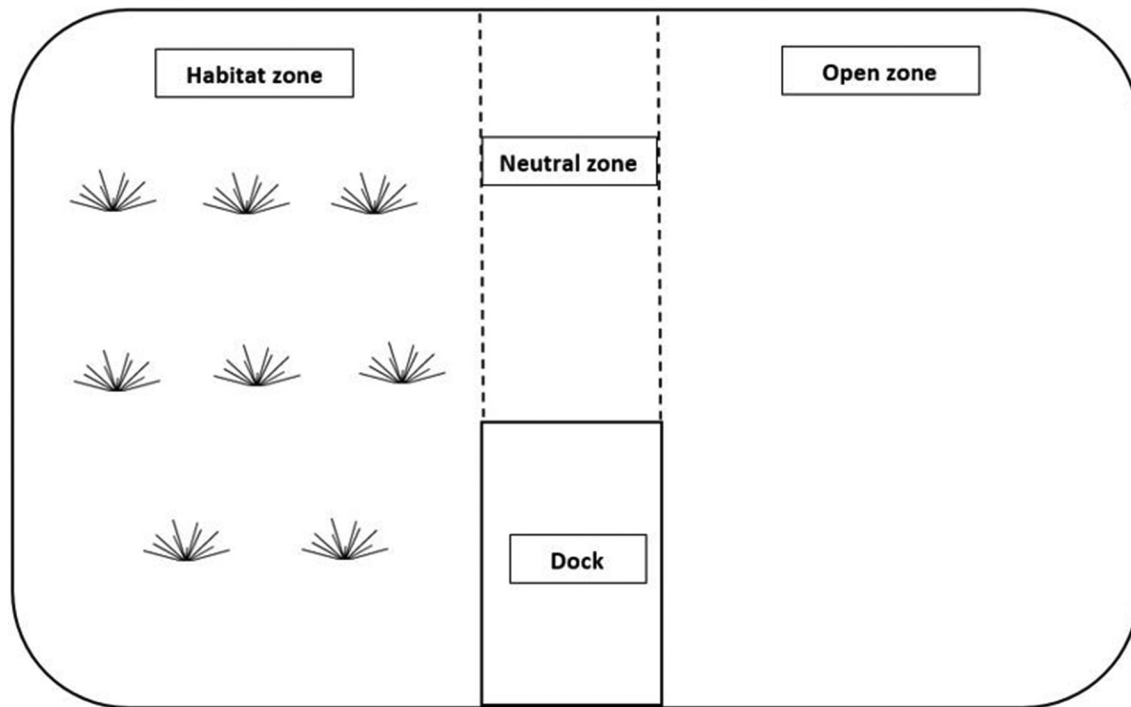
After all behavior assays were complete, largemouth bass were haphazardly stocked into one of three 0.04 ha ponds (2 m depth, 24 m length, and 15 m width) on 8 June 2018 ($n = 44$ per pond). Experimental ponds were drained prior to stocking to allow benthic sediment to air-dry for 7 days, thereby minimizing the abun-

dance of aquatic plants and benthic invertebrates. Ponds were then refilled and angling began 10 days later. Submerged and emergent vegetation was minimal, and vegetative cover was similar across the ponds, although not specifically quantified.

Each pond was divided into three sections: one section (termed structured habitat) comprised approximately 45% of the pond area that contained artificial structure; a second section (termed the open habitat) comprised approximately 45% of the pond area that contained no supplemental habitat; a third section (termed the neutral zone) comprised approximately 6% of the total area between the two other sections. The structured habitat contained eight evenly spaced porcupine attractors in the benthic zone (Fig. 1). Each porcupine attractor was made with eight, 1.3 cm diameter, 1.5 m long PVC pipes secured within a cement-filled plastic container (0.6 m length \times 0.3 m width \times 0.3 m height) as the base. These porcupine attractors mimic the design and complexity of evergreen trees, and they have been shown to increase largemouth bass abundance at similar rates to evergreen trees and other manufactured fish attractors (Baumann et al. 2016). In addition, artificial structures such as these have previously been used to attract fish, increase fish density, and increase angling catch rates (Rogers and Bergersen 1999; Bolding et al. 2004; Smokorowski and Pratt 2007). Benthic vegetation was allowed to grow freely within the structured habitat, although vegetation was limited due to the dry-out period prior to the start of the study and the relatively brief duration of the angling portion of the study (a total of 15 days). The open habitat had multiple 3 m \times 15 m black Lake Bottom Blanket (Wayne, New Jersey, USA; available from <https://lakebottomblanket.com/>) benthic liners atop the substrate to prevent aquatic plant growth and provided no refuge for the largemouth bass. The liner covered approximately 90% of the pond's open habitat. The neutral zone between the two treatment habitats had no artificial structure and no benthic liner, allowing natural vegetation to grow, but was not targeted by anglers during angling trials, thereby acting as a buffer to increase the confidence of assigning an angled fish to either the structured habitat or the open habitats of the pond. Together, this experimental design for the pond study contained areas of structured habitat and open habitat, and thus mimicked the arenas where behavioral assays were performed (i.e., a refuge zone and an open zone), increasing the likelihood of having inter-individual laboratory-based behaviors carry over into field trials (Mazué et al. 2015). In addition, studies have found largemouth bass home ranges to be very variable in size, ranging from 0.0009 to 5.16 ha (Lewis and Flickinger 1967; Winter 1977; Mesing and Wicker 1986). Therefore, it is possible that largemouth bass in this study may have formed home ranges within our 0.04 ha experimental ponds.

All ponds were stocked with approximately 2000 forage fish each, made up of a combination of fathead minnows (*Pimephales promelas* Rafinesque, 1820) (subset mean (\pm SD) total length = 51 \pm 5.0 mm) and golden shiners (*Notemigonus crysoleucas* (Mitchill, 1814)) (subset mean (\pm SD) total length = 65 \pm 5.4 mm) 1 day prior to stocking largemouth bass. Fathead minnows and similar species are commonly used as prey items in predation experiments (Chivers et al. 2007; Ahrens et al. 2012), and previous studies in laboratory settings showed that largemouth bass of the size used in the current study can consume minnows of this size (Midway et al. 2017). Mean (\pm SD) temperature was 27.0 \pm 2.3 °C across all three ponds, mean (\pm SD) dissolved oxygen concentration was 6.2 \pm 2.8 mg/L, and mean (\pm SD) turbidity (measured with a Secchi disk) was 99.5 \pm 20.6 cm. Mean (\pm SD) total length of stocked largemouth bass was not different across the ponds ($TL_A = 282 \pm 19$ mm, $TL_B = 282 \pm 23$ mm, $TL_C = 280 \pm 21$ mm, where A, B, and C are ponds; one-way analysis of variance (ANOVA), $F_{[2,115]} = 0.121$, $p = 0.887$). Stocked largemouth bass remained in these ponds for a total of 15 days, with 9 days for acclimation and 6 days during which angling occurred.

Fig. 1. Overhead view of the experimental pond design. The pond was approximately 24 m long × 15 m wide. Each of the three replicate ponds had (i) a structured habitat (approximately 10 m in width), (ii) an open habitat (approximately 10 m in width), and (iii) a neutral zone (approximately 4 m in width) separating the structured habitat and the open habitat, which extended from the dock. Note that the drawing is not to scale.



Daily angling sessions began on 17 June 2018 and concluded on 22 June 2018, with 1 day where no angling occurred (on 21 June 2018). Each daily session consisted of 20 min of angling in each pond, including handling time for all captured fish. All sessions took place between the hours of 0815 and 0945 and were completed by the same two experienced anglers (M.J.L. and C.D.S.). Angling gear consisted of a medium-action spinning rod and reel spooled with clear, 2.7 kg test monofilament fishing line. One lure type was used for the entire study: a size two weedless hook with a 7.6 cm watermelon-colored with red flakes plastic Yum dinger worm, rigged “wacky style”, appropriate for the size of largemouth bass used in this study. The order in which the three ponds were fished each day was decided with a random number generator, both anglers fished concurrently in the same pond, and only one angler at a time fished the structure or no structure sections. Upon arriving at the designated starting pond, a coin flip was used to assign anglers to a section of the pond (structured habitat or open habitat), and anglers were free to choose a starting location around the perimeter of the pond. Anglers started fishing at the same time and they were free to move around the perimeter of their assigned section, cast, and attempt to pass their lures through all areas of their section, thereby ensuring that all fish within the pond would be presented with the lure. Anglers fished in a way that was common when targeting largemouth bass with lures of this kind (i.e., lures casted and retrieved slowly, a “hook set” occurred when the angler believed a fish had struck the lure), and care was taken to attempt to have anglers fish in a similar, consistent fashion throughout the study. Each captured largemouth bass was identified by a PIT tag before being released back into the pond in less than 1 min after capture, allowing for recaptures to occur. Records indicated instances where minor bleeding occurred or deeply hooked fish were released with the hook in place ($n = 6$ captures) (Stein et al. 2012). The occurrence of “misses” was also recorded when anglers hooked a fish, but the fish rejected the hook and was not captured, such that misses and cap-

tures were considered separate metrics. Altogether, each pond received 5 days of angling during the study.

The same day that angling trials concluded, ponds were drained and between 38 and 42 of the 44 originally stocked fish were recovered from each of the study ponds ($n = 121$ recovered fish from a total of 132 total stocked; 92% recovered). Fish found dead, or that were not recovered during pond draining, were excluded from subsequent analyses. All methodology was in accordance with the *Guide to the Care and Use of Experimental Animals* and approved by the University of Illinois Institutional Animal Care and Use Committee (IACUC protocol No. 17160).

Statistical analysis

Intra-class correlation coefficient (ICC) analysis, with a two-way ANOVA design suited for a single rater, was first used to determine individual repeatability of the five recorded behaviors quantified during behavioral assays in the arenas (Shrout and Fleiss 1979; Bell et al. 2009). Principal components analysis (PCA) was then used to distill repeatable behaviors and ensure correlated variables did not inflate other statistical models (Budaev 2010). Principal components with eigenvalues >1 were extracted and rotated, and factor loadings above 0.4 were used for interpretation (Hair 1998; Ho 2006; Budaev 2010).

A logistic regression with a binomial error distribution was used to test for differences in the proportion of fish captured between the structured habitat and the open habitat across study ponds (Crawley 2013). A multinomial regression, defined as a logistic regression with three or more categorical outcomes (captured in structured habitat, captured in open habitat, or captured in both habitats), was used to test for the influence of pond, angler, and PC score on the habitat where captures occurred (Bolker et al. 2008). To discern differences in the behavioral phenotypes of captured fish, a linear mixed-effects model was used that included the interaction between angling day and pond habitat where capture occurred as fixed effects and angler and pond as random

Table 1. Results of intra-class correlation (ICC) analysis to define repeatability of five behaviors generated during laboratory assays with largemouth bass (*Micropterus salmoides*).

Behavior	Mean \pm SD	Median	Range	Repeatability	Confidence interval	<i>p</i>
Swim activity pre-predator (s)	342 \pm 104	346	8.5–566	0.245	0.068 < ICC < 0.407	0.004
Time spent in center pre-predator (s)	141 \pm 116	108	9–591	0.472	0.319 < ICC < 0.601	<0.001
Swim activity post-predator (s)	239 \pm 98.2	249	6–436	0.395	0.232 < ICC < 0.537	<0.001
Time spent in center post-predator (s)	109 \pm 104	77.5	0–526	0.487	0.337 < ICC < 0.613	<0.001
Freeze time (s)	64.8 \pm 73.5	42	3–398	0.167	–0.013 < ICC < 0.337	0.035

Note: Confidence intervals and *p* values (with *p* < 0.05 set in boldface type) show the strength in the repeatability for each behavior.

Table 2. Principal component (PC) analysis, factor loadings, and variance for repeatable behaviors generated from laboratory assays with largemouth bass (*Micropterus salmoides*).

Factor	PC1 loadings
Swim activity pre-predator (s)	–0.511
Time spent in center pre-predator (s)	0.585
Time spent in center post-predator (s)	0.538
Eigenvalue	2.28
% Variance explained	57.01

Note: The behaviors measured, as well as intra-class correlation analyses to quantify repeatability, are given in Table 1. Factor loadings above 0.4 are shown, as behaviors above this threshold can be used to explain relationships between factors within a PC.

effects (Bolker et al. 2008). Lastly, a generalized linear mixed-effects model was used to define the effects of behavior and habitat on the number of times individual fish were captured, with PC scores and habitat as fixed effects and angler, pond, and fish ID as random effects. Size (total length) was added as a fixed effect to the linear and generalized linear mixed-effect models because size has previously been shown to influence the likelihood of capture (Vainikka et al. 2016) and (or) behavioral score (Krause et al. 1998).

To quantify differences in behavior distributions and number of times individual fish were captured across the three ponds, two separate one-way ANOVAs were used, one with PC score as the response variable and pond as the main effect, and a second with the number of times individual fish were captured as the response variable and pond as the main effect. To define differences in the proportion of captures and misses between anglers across the study ponds, a logistic regression model with binomial error distribution was used (Crawley 2013). A Poisson regression, recommended for count data, was used to quantify differences in the total number of captures across angling sessions (Bolker et al. 2008). To quantify any effects of angler and pond on the behavioral phenotypes of captured fish, a two-way ANOVA was used that included the PC scores of captured fish as the response variable and angler, pond, and their interaction as fixed effects.

All analyses were conducted in R (version 3.4.1), including packages Tidverse version 1.2.1 (Wickham 2017), irr version 0.84 (Gamer et al. 2012), psych version 1.8.12 (Revelle 2018), vegan version 2.5-3 (Oksanen et al. 2018), readr version 1.2.1 (Wickham et al. 2018), lme4 version 1.1-15 (Bates et al. 2015), nnet version 7.3-12 (Venables and Ripley 2002), car version 2.1-6 (Fox and Weisberg 2011), coefplot version 1.2.6 (Lander 2018), lsmeans version 2.30-0 (Lenth 2016), ggplot2 version 3.1.0 (Wickham 2009), and gridExtra version 2.3 (Auguie 2017). Statistical significance was determined at $\alpha = 0.05$.

Results

Of the five behavioral variables measured, ICC analyses confirmed that pre-predator swimming activity, pre-predator open zone, post-predator swimming activity, and post-predator open zone were repeatable, with repeatability values above 0.2 and confidence intervals that did not include zero (Table 1). Freeze times were not repeatable and were therefore not included in PCA (Table 1). One principal component (PC1) was extracted from the repeatable behaviors (Table 2). PC1 explained 57% of the behavior variation and had an eigenvalue of 2.28 (Table 2). The mean PC1 score was -8.47×10^{-12} , the median was -0.45 , and the range was -2.19 to 6.51 . Largemouth bass with high PC1 scores were less active during pre-predator simulation and spent a lot of time in the open zone (bold) during both pre- and post-predator simulation, while fish with low PC1 scores were highly active and spent very little time in the open zone (shy).

The PC1 score of captured fish did not differ significantly across angling sessions (Table 3, Fig. 2). Furthermore, there was no difference in the PC1 scores of largemouth bass captured only in one pond habitat, captured in both pond habitats, or fish that were not captured (Table 3, Fig. 3). Total length and PC1 correlated positively such that larger fish were less active and bolder relative to smaller largemouth bass (Table 3, Supplementary Fig. S1¹). Angler had a significant influence on the pond habitat where fish were captured, with fish captured by both anglers (M.J.L. and C.D.S.) more likely to be captured in both the structured habitat and the open habitat when compared with fish captured only by M.J.L. or only by C.D.S. (Table 4, Fig. 4A). The number of times a fish was captured differed by pond habitat type (Fig. 4A, Supplementary Table S1¹). Specifically, fish captured once were equally likely to be captured in either the structured habitat or the open habitat, but fish captured more than once were significantly more likely to have been captured in both the structured habitat and the open habitats, rather than having multiple captures within a single pond habitat. Neither PC1 score nor fish size influenced the number of individual captures, and neither differed between captured and uncaptured fish (Fig. 4B, Supplementary Table S1¹).

Across the five angling sessions, a total of 112 captures occurred, with 51 fish captured only once, 26 fish captured twice, and 3 fish captured three times. There was no significant difference in proportion of total captures between the structured habitat ($n = 55$ captures; 49%) and the open habitat ($n = 57$ captures; 51%) across all ponds (logistic regression, $z = -0.433$, $df = 2$, $p = 0.665$). The proportion of total captures, as well as the proportion of total misses, did not differ significantly across the two anglers, accounting for the three different ponds used in the study; C.D.S. had a total of 12 misses and 56 captures and M.J.L. had a total of 18 misses and 56 captures (logistic regressions for misses: $z = 0.327$, $df = 2$, $p = 0.744$; logistic regression for captures: $z = -0.835$, $df = 2$, $p = 0.403$). The total number of captures was significantly different across angling sessions, with 43 captures during session 1, 30 captures during session 2, and then between 8 and 18 captures in each of sessions 3 through 5 (Supplementary Table S2¹). Neither

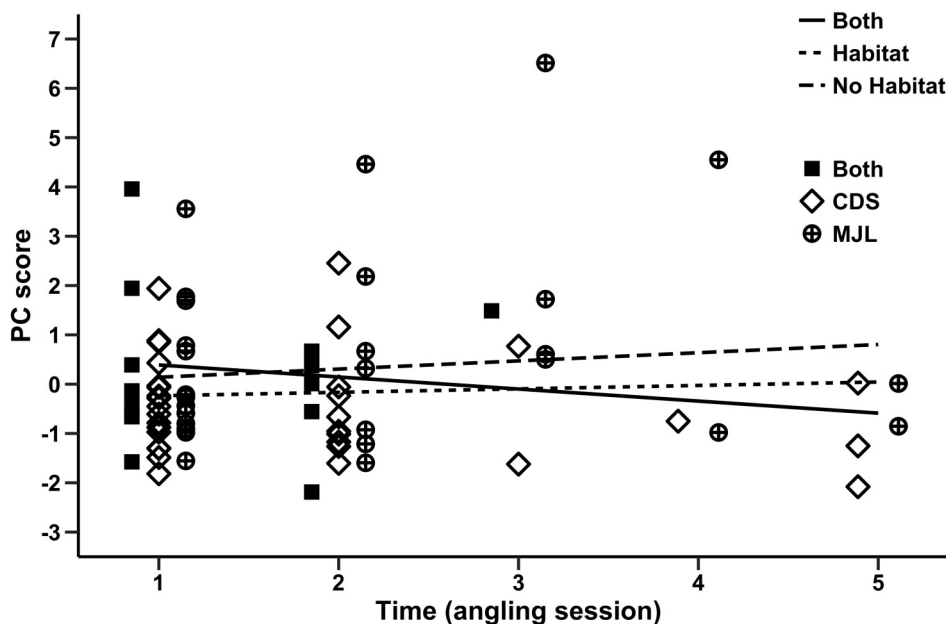
¹Supplementary tables and figures are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0191>.

Table 3. Results of linear mixed-effects model showing effects of angling session, habitat type, and total length (mm) on principal component scores of captured largemouth bass (*Micropterus salmoides*).

Variable	Parameter estimate	SE	df	t	p	r^2_m	r^2_c
Angling session	-0.110	0.485	69.637	-0.228	0.821	0.182	0.237
Structured habitat	-1.259	1.031	69.214	-1.222	0.226		
Open habitat	0.107	1.034	69.284	0.103	0.918		
Total length (mm)	0.033	0.009	69.491	3.759	<0.001		
Angling session × structured habitat	0.385	0.524	69.096	0.735	0.465		
Angling session × open habitat	0.026	0.545	68.488	0.047	0.962		
Random effects		Variance	SD				
Pond (intercept)		0.004	0.060				
Angler (intercept)		0.150	0.387				
Residual		2.111	1.453				

Note: Pond and angler were included in the model as random effects. The r^2_m is the marginal coefficient of determination, which represents the proportion of variance described by only the fixed factors, and r^2_c is the conditional coefficient of determination, which represents the proportion of variance that can be described by both fixed and random factors.

Fig. 2. Differences in principal component (PC) scores of largemouth bass (*Micropterus salmoides*) captured across five different angling sessions in three replicate ponds. The short-dashed line shows the change in PC score across angling sessions for largemouth bass captured exclusively in the structured habitat, the long-dashed line shows the change in PC score for largemouth bass captured in the open habitat, and the solid line shows the change in PC score over angling sessions for largemouth bass captured in both pond habitats. Symbol shape represents fish captured by C.D.S. (open diamond), M.J.L. (circle with plus sign), or both anglers (solid square).



mean (\pm SD) PC1 score nor total number of times individual fish were captured differed significantly across ponds ($PC1_A = -0.117 \pm 1.0$, $PC1_B = 0.184 \pm 1.8$, $PC1_C = -0.041 \pm 1.6$, one-way ANOVA, $F_{[2,115]} = 0.392$, $p = 0.677$; mean (\pm SD) number of times individual fish were captured in ponds: A = 0.975 ± 0.77 , B = 0.857 ± 0.85 , and C = 0.860 ± 0.80 , one-way ANOVA, $F_{[2,115]} = 0.275$, $p = 0.76$). Angler had a significant effect on the behavior types that were captured, whereby the PC1 scores of the C.D.S. captures were significantly lower than the PC1 scores of the M.J.L. captures, indicating that C.D.S. captured highly active, shy fish compared with those that M.J.L. captured (Table 5, Supplementary Fig. S2¹).

Discussion

Activity and boldness behaviors did not predict any aspect of angling vulnerability for largemouth bass in this study. Repeatable laboratory-derived behaviors formed a single principal component that consisted of measures of activity and boldness. This

PC score did not significantly predict the number of times that fish were captured, and the PC score of captured fish did not differ from that of uncaptured fish. Furthermore, the PC score of captured fish did not change across the five angling sessions. Not all fish strike fishing lures, and there are many factors known to influence angling vulnerability including the probability of a fish encountering a lure, the metabolic rate of the fish, and behavioral phenotype (i.e., individual boldness or activity) (Härkönen et al. 2014; Arlinghaus et al. 2017a; Lennox et al. 2017; Monk and Arlinghaus 2017). The five established animal personality axes are aggression, sociability, activity, exploration, and boldness (Réale et al. 2007), and these behaviors differ between individual fish and have a heritable, genetic component (Mazué et al. 2015). Behavioral phenotypes are particularly important for fisheries because past studies have shown that behavioral phenotype can cause some fish to be predisposed to capture through angling, and more importantly, anglers have the potential to artificially select for

Fig. 3. Distribution of principal component (PC) scores for largemouth bass (*Micropterus salmoides*) captured in the open habitat, structured habitat, captured in both structured habitat and open habitats (both), or were uncaptured. The thick vertical lines inside the boxes show the median, the diamonds represent the mean, the whiskers represent the upper and lower quartiles \pm the interquartile range, and the open triangles represent outliers with values less than the first quartile minus 1.5 times the interquartile range or greater than the third quartile plus 1.5 times the interquartile range. Behavioral metrics that make up the PC score were repeatable and are shown in Table 1.

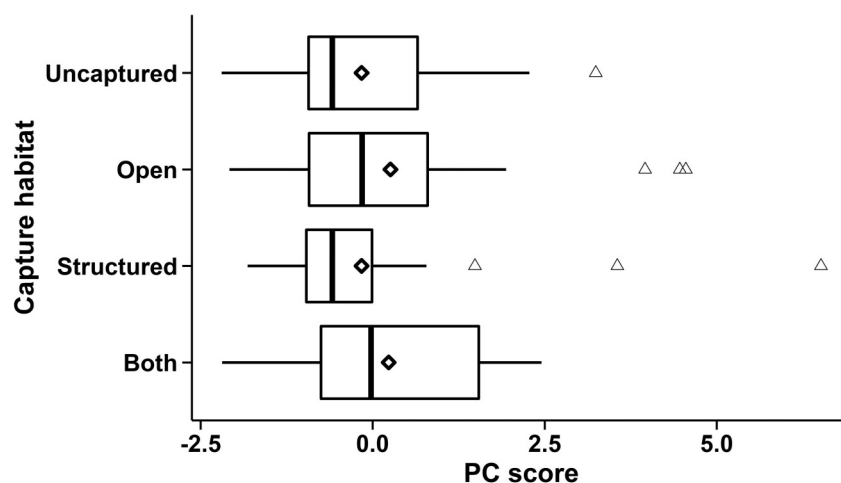


Table 4. Summary of multinomial regression explaining in which habitat in the pond that largemouth bass (*Micropterus salmoides*) were captured across five angling sessions in three replicate ponds.

Variable	LR χ^2	df	<i>p</i>
PC score	2.752	2	0.253
Pond	1.779	4	0.776
Angler	13.492	4	0.009

Note: Principal component (PC) score, pond, and angler were the predictor variables in the multinomial regression, and the dependent variable was the pond habitat where fish were captured (either the open habitat, the structured habitat, or both). A diagram of the pond is shown in Fig. 1; the measured behaviors to generate PC scores are shown in Table 1; the results of PC analyses are given in Table 2. Angler (set in boldface type) was the only predictor variable with a significant influence on the pond habitats where largemouth bass were captured ($p < 0.05$). LR is likelihood ratio.

fish of specific behavioral phenotypes (Cooke et al. 2007), decreasing genotypic diversity (Uusi-Heikkilä et al. 2015), and reducing capture rates (Kuparinen and Merilä 2007). Previous work linking behavioral metrics to angling vulnerability has been inconsistent; patterns emerging from some studies are not repeated in other work. For example, activity within a natural lake, measured by acoustic telemetry, did not predict angling vulnerability of Eurasian perch (Monk and Arlinghaus 2018), whereas a study using laboratory-measured activity in hatchery-reared brown trout (*Salmo trutta* Linnaeus, 1758) found that the most active fish were the most vulnerable to angling (Härkönen et al. 2014). For boldness, bolder rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) (Biro and Post 2008) and common carp (*Cyprinus carpio* Linnaeus, 1758) (Klefoth et al. 2017) were both shown to be more vulnerable to capture than their shy conspecifics, whereas the opposite was found for bluegill, with shy bluegill being more vulnerable to angling (Wilson et al. 2011). However, studies relating behavioral traits to capture in largemouth bass specifically seem to be consistent, since several studies have failed to demonstrate a link between activity and boldness behaviors and capture for this species (Binder et al. 2012; Louison et al. 2017; present study), with angling vulnerability more strongly linked to cortisol responsiveness and learning (Louison et al. 2017, 2019). Because largemouth bass are sit-and-wait predators that often remain stationary and

wait for prey items to appear before them, particularly in structured habitats (Savino and Stein 1982), activity and boldness may not play a role in their foraging strategy, and therefore may not influence encounters and strikes with fishing lures in all habitat types. Rather, for largemouth bass, upon having a lure appear in front of them, their decision to strike appears to be more strongly influenced by cortisol responsiveness (Louison et al. 2017), rather than boldness or activity metrics. Several studies have shown that, when protecting their broods, aggression (defined as the probability for a fish to attack conspecifics or defend territory; Réale et al. 2007; Koolhaas 2008) will play a role in the decision by male largemouth bass to strike a fishing lure (Suski and Philipp 2004; Sutter et al. 2012). However, this relationship is complicated by the fact that aggression and lure striking during the brood guarding period are influenced by both individual size and brood size, such that larger (older) males, presumably closer to the end of their reproductive life, that have larger broods engage in more aggressive nest defense relative to small males with small broods, increasing the likelihood that these large males strike a lure when it is near their nest (Suski and Philipp 2004; Sutter et al. 2012). Relationships between aggression and lure striking outside of the brood guarding period have not been explored for largemouth bass, and the presence of this relationships for females has not been defined, providing opportunity for future studies. Together, results from this study indicate that activity and boldness behavioral traits do not predict capture in largemouth bass.

The total proportion of largemouth bass captured, as well as the number of times that individuals were captured, were similar between the open habitat and the structured habitats of the ponds. Habitat is a key aspect of fish growth and survival, with many fish commonly found in association with habitat (Lima 1998; Hollins et al. 2018). As a result, many management programs are predicated on building, restoring, or enhancing habitat, often with artificial structures, in an effort to enhance fish populations, encourage growth, and improve angler catch rates (Smokorowski and Pratt 2007; Baumann et al. 2016). Previous work with largemouth bass has found that artificial habitat can attract fish, increase densities, and also increase angler catch rates (reviewed in Bolding et al. 2004). In addition, work by Baumann et al. (2016) showed that the addition of porcupine attractors increased fish abundance compared with control sites, but angling was not used to link this increased abundance to influences on catch rates. There are three possible explanations as to why we did not see

Fig. 4. (A) The number of times that individual largemouth bass (*Micropterus salmoides*) were captured across all pond habitats, including uncaptured fish and fish captured in both the open habitat and the structured habitats. The color of the data points represents the angler that captured the fish, including uncaptured fish and fish captured by both anglers. Note that the y axis in is a category (zero, one, two, or three captures), but data points have been jittered to avoid over-plotting and allow visualization of all data. (B) The relationship between the principal component (PC) scores and the number of times that largemouth bass were captured during five angling sessions across three replicate ponds, with zero used to represent uncaptured fish.

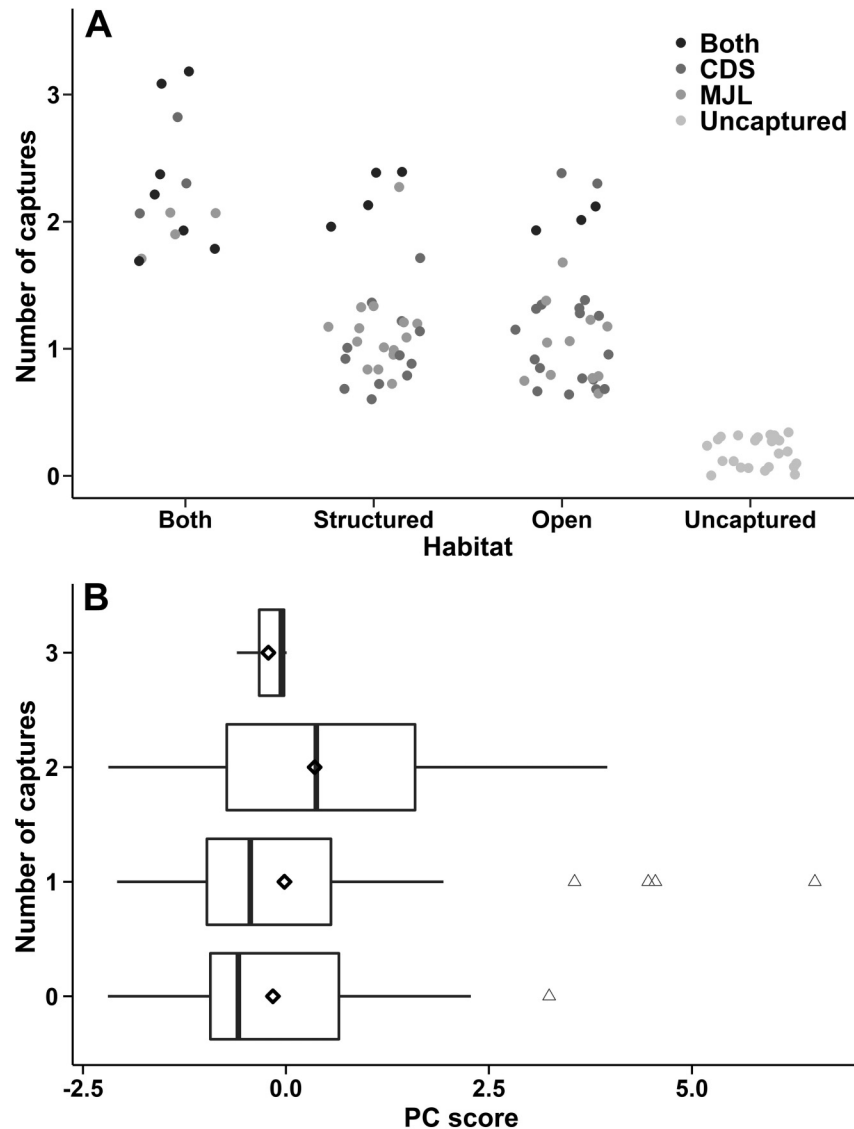


Table 5. Summary of a two-way ANOVA testing for effects of angler, pond, and their interaction on the principal component (PC) scores of captured largemouth bass (*Micropterus salmoides*).

Predictor variable	F	df	p
Angler	3.36	2	0.041
Pond	0.29	2	0.751
Angler × pond	0.31	4	0.873

Note: Angler (set in boldface type) was the only predictor variable with a significant influence on the PC scores of captured largemouth bass ($p < 0.05$).

differences in capture metrics between the structured habitat and the open habitats of our ponds. First, it is possible that the habitat that we used (PVC tubes) was not sufficiently structurally complex and did not have small interstitial spaces, which are known to be more effective at aggregating largemouth bass (Bolding et al.

2004), such that largemouth bass did not associate with these structures. However, porcupine attractors are commonly used to successfully aggregate fish, and enhance fisheries when compared with control environments with no habitat additions (Baumann et al. 2016), suggesting that the association of largemouth bass with structure of this type is possible. Second, the small pond size (approximately 0.04 ha), relatively short duration of the study, and lack of predators may have allowed largemouth bass to use the entire pond for foraging without the perceived risk of being preyed upon, making it difficult to detect differences in habitat use through angling (Lima 1998). Finally, it is possible that the addition of habitat could have resulted in an increase in fish abundance in the structured habitat, but abundance or residence patterns were not measured (only capture). Fish abundance and angler catch rates are not always related (Wegener et al. 2018) and catch rates in some fisheries remain high even when abundance of fish is low (Erisman et al. 2011). As such, largemouth bass densities may have been different across the two sections of our

ponds, but this difference may not have translated into noticeable differences in catch rates. Future work on this topic should explore how different habitat types can influence habitat selection in largemouth bass, ideally working with wild largemouth bass and in larger environments over extended time periods to increase knowledge about space, habitat use, previous exposure to fishing lures, and possible influences of conspecific competition for this species. Regardless of the mechanism, results from this study demonstrate that the proportion of largemouth bass captured by anglers did not differ between areas of the pond that received supplemental additions of porcupine attractors relative to habitats where no artificial structures were added.

The behavioral phenotype of largemouth bass did not predict the pond habitats where captures occurred, and largemouth bass captured by anglers did not exhibit habitat preferences across behavioral phenotypes. The behavioral phenotype of largemouth bass did not differ between fish captured in either the open habitat or the structured habitats, fish captured multiple times across habitats (rather than being caught in only one habitat), and uncaptured fish. Previous work has shown that behavioral phenotypes of fish, such as boldness and activity, are consistent within individuals, and that shy fish tend to spend more time in sheltered habitats than bolder conspecifics (Hollins et al. 2018). As such, prior to starting this study, we predicted that fish of certain behavioral phenotypes would have associated with different habitat types, which would have resulted in PC scores for captured fish differing across capture locations. Previous work with bluegill, for example, found a relationship between habitat use and behavior, with bold bluegill spending more time in open areas away from refuges compared with their shy conspecifics that spent more time in refuge areas (Wilson et al. 2011). A study with Eurasian perch found a similar result, in which habitat choice strongly influenced capture vulnerability, whereby fish were more vulnerable to capture in specific spatial locations of their study lake (Monk and Arlinghaus 2018). However, the most highly vulnerable perch with the most captures were not repeatedly captured in the same habitat types (Monk and Arlinghaus 2018), similar to results shown here. In the current study, potential reasons for not finding a relationship between behavioral phenotypes and habitat types as predicted are likely due to the small size of the ponds or lack of direct translation from boldness behaviors measured in the laboratory to habitat selection behaviors within the study ponds (Toms et al. 2010; White et al. 2013). It is also possible that the interaction between behaviors and habitat selection do not exist and therefore cannot determine angling vulnerability of largemouth bass, which warrants further investigation in future studies. Together, results show that largemouth bass of all behavioral phenotypes were using all available habitats (both open habitats and structured habitats), and that habitat selection is likely not a product of the two behavioral phenotypes measured in this study (i.e., boldness and activity).

Unexpectedly, the behavioral phenotypes of captured largemouth bass was significantly different between the two anglers. More specifically, M.J.L. captured fish with significantly higher PC scores, indicating less active and bold laboratory-based behaviors caught compared with C.D.S., and this difference was consistent across the three replicate ponds. This study was designed in a way to minimize differences in angler effects, including care taken to ensure both anglers fished in the same systematic and standardized way, both anglers using a single identical lure, and the use of randomized angling assignments during each session. In addition, based on the fact that there were no differences in either proportion of captures or proportion of misses, it is reasonable to assume that both anglers were similar in terms of skill. Other studies have found positive relationships between angler skill level, size of fish captured, and hooking depth, where skilled anglers captured larger Eurasian perch (Monk and Arlinghaus 2018) and hooked smallmouth bass (*Micropterus dolomieu* Lacepède,

1802) deeper than unskilled anglers (Dunmall et al. 2001), indicating that different types of anglers can result in differences in fishing outcomes. In the current study, one possible explanation for why anglers of similar skill levels captured fish with different behavioral phenotypes may be related to subtle differences in angler fishing techniques or reaction times, measured between the time that fish strike lures and when the anglers set their hooks (Gutowsky et al. 2017). Fish differ in their willingness to taste, bite, and reject fishing lures (Monk and Arlinghaus 2017), as well as their approach to a fishing lure (aggressive vs. passive), and anglers can have different reaction times or fishing styles, such that this interaction can lead to capture of different behavioral phenotypes between anglers. For example, C.D.S. may have had longer delays before setting the hook, or had longer reaction times, leading to the capture of only active fish that continued swimming after striking or aggressively ingesting the lure. In contrast, M.J.L. may have allowed less time to pass before setting his hook following the detection of a strike, resulting in him capturing more inactive fish that did not strike forcefully. However, the direct relationship between angler approach and behavior traits of captured fish was not explicitly quantified in the current study, making conclusions of this nature somewhat speculative. Better defining the relationship between the anglers and the potential for directional selection should be explored in more detail in the future. Overall, this difference in behavioral score across anglers suggests that selection pressures on fisheries may be more complex than previously thought, owing to behavioral differences of captured fish between individual anglers, even of the same skill level.

Results from this study have three main implications for fisheries management. First, findings suggest that there will be minimal selection on activity and boldness behaviors of largemouth bass by anglers, with these two behaviors having little influence on the probability of capture regardless of habitat type. Previous work has suggested that angling has the potential to disproportionately remove bold individuals from the population leaving only shy fish, a condition often referred to as the timidity syndrome (Biro and Post 2008; Arlinghaus et al. 2017). However, results from the current study do not support this hypothesis, but they concur with previous work with largemouth bass showing that boldness behavior has little impact on angling vulnerability for this species (Louison et al. 2017), indicating that the disproportionate removal of bold individuals by anglers would not be expected. It is possible that selection on other factors could occur (i.e., cortisol responsiveness, learning, aggression during the brood guarding phase; Suski and Philipp 2004; Sutter et al. 2012; Louison et al. 2017, 2019) that could lead to reduced capture rates and (or) FIE, and future work should quantify additional behavioral axes not measured here (i.e., sociability, conspecific aggression outside of the reproductive period) with experiments conducted over longer time scales (i.e., several generations) to define changes to phenotypes or genotypes with extended angling pressure. Second, this study did not find capture rates to be higher in the structured habitat of the ponds with porcupine attractors present. Because the goal of many management projects is to introduce artificial structures to supplement habitat restoration, attract fish, and increase catch rates, management activities aimed at increasing capture rates of largemouth bass should consider structures other than porcupine attractors, including those with more interstitial space (Bolding et al. 2004; Baumann et al. 2016). Lastly, individual anglers may be influencing capture of fish with certain behavioral and physiological traits, even between anglers of similar skill levels. Selection pressures based on angler technique and (or) skill level should be investigated in further detail to discern the influence of angler behavior on the phenotypes of captured fish. These angler differences pose a unique challenge by increasing the complexity to achieve effective fisheries management that can be applied to all types and skill levels of anglers.

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