



Big, hungry fish get the lure: Size and food availability determine capture over boldness and exploratory behaviors

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ABSTRACT

Fish behavioral phenotypes have previously been shown to influence capture by recreational anglers, and artificial selection of specific phenotypes can occur. However, little is known about how environmental conditions influence which phenotypes are most vulnerable. This study sought to define the interaction between behavioral phenotype and prey availability to influence angling vulnerability using largemouth bass, *Micropterus salmoides* (Lacepède). Behavioral assays to define boldness and exploratory phenotype were performed, and fish were transferred to one of two ponds for angling; fathead minnows, *Pimphales promelas* (Rafinesque) were stocked as prey into one pond while the other pond had no minnows. Behavioral phenotype did not influence capture, regardless of prey availability, and catch rates were higher in the pond that had no minnows relative to the pond with minnows. Size was the strongest predictor of capture, with larger fish most likely to be captured, despite a narrow range of total lengths across all individuals. Findings suggest that angling of largemouth bass is not influenced by exploration and boldness behavioral phenotypes, no matter the prey density.

1. Introduction

Fish have previously been found to demonstrate consistent, repeatable and heritable differences in behaviors known as behavioral syndromes (Bell, 2007), with behaviors being grouped into five axes (boldness, exploration, sociability, activity and aggression; Réale et al., 2007; Conrad et al., 2011). Research has also found that these syndromes can be influenced by environmental conditions (Ruiz-Gomez et al., 2008; Dingemanse and Wolf, 2010; Killen et al., 2013). More specifically, environmental context can influence a fish's behavior, resulting in behavioral shifts often referred to as behavioral plasticity (Killen et al., 2013). One example of behavioral plasticity due to environmental context relates to food availability, where food shortages created increased variability in boldness behaviors of European sea bass, (*Dicentrarchus labrax*) during foraging (Killen et al., 2016). An additional example of behavioral plasticity due to environmental context is a 2.5- to 6-fold increase in boldness behaviors of speckled damselfish, (*Pomacentrus bankanensis*) when temperatures were raised from 24 °C to 27 °C (Biro et al., 2010). Clearly, individual fish behavior can change with environmental context.

Behavior has also been shown to play a large role in influencing vulnerability to hook-and-line angling (Lennox et al., 2017). Simply encountering a bait is not sufficient to cause a fish to strike (Monk and

Arlinghaus, 2017), and lure-striking decisions by fish result from the combination of a number of factors that include encountering angling gear, the interaction of the fish with the angling gear, and internal characteristics of the fish, including aspects of behavioral syndromes and correlated traits, such as metabolic rates (Lennox et al., 2017; Stoner, 2004). More specifically, work with both fish (rainbow trout, *Oncorhynchus mykiss*, (Biro and Post, 2008); common carp, *Cyprinus carpio* (Klefoth et al., 2017); rock bass, *Ambloplites rupestris* (Fedele, 2017)), as well as crayfish (common yabby, *Cherax destructor*, (Biro and Sampson, 2015) has shown that bold and exploratory behavioral phenotypes can be more vulnerable to capture by humans than shy behavioral phenotypes, though this finding does not occur in all species, including bluegill (*Lepomis macrochirus*) (Wilson et al., 2011; Mittelbach et al., 2014). In addition, hunger from reduced food intake can increase risk-taking and exploratory behaviors (Beukema, 1968), which can lead to increased capture rates (Härkönen et al., 2014; Lennox et al., 2017). Larger fish are often behaviorally dominant to smaller fish (Krause, 1994), which could lead to increased capture of larger fish. Importantly, the repeated removal of fish with specific, heritable behavioral traits by anglers (i.e., bold or active individuals; Biro and Post, 2008) has the potential to result in behavioral changes to populations over the long term (Cooke et al., 2007; Heino et al., 2013; Alós et al., 2016), often referred to as the timidity-syndrome (Arlinghaus et al.,

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2017). Thus, if angling preferentially selects and removes bold phenotypes from a population, over many generations due to the heritability of angling vulnerability (Philipp et al., 2009), it may be that only shy individuals with lower angling vulnerability remain. Angling therefore has the potential to render fish populations less catchable overall (Philipp et al., 2009) due to timidity-syndromes (Arlinghaus et al., 2017), making mechanisms of vulnerability an important concept for managers to consider to conserve, protect, and enhance recreational fish stocks.

While a number of potential mechanisms explaining angling vulnerability in the context of behavior have been proposed (Lennox et al., 2017; Stoner, 2004), findings and trends across studies have been variable and inconsistent, and many factors predicting angling vulnerability have not been explored, limiting our ability to predict how harvest by anglers can shape populations. For example, most studies to date that focus on angling vulnerability have used only a single behavioral trait (typically boldness), limiting the ability to define the relative importance of different behavioral traits on vulnerability. In addition, most work on this topic has focused on behavioral phenotypes and angling vulnerability within a single, stable environment, ignoring the dynamic nature of both abiotic and biotic environmental factors, precluding the ability to define the role of environmental conditions and behavioral plasticity on vulnerability (Sih and Bell, 2008; Lennox et al., 2017). But, certain behavioral phenotypes may be highly vulnerable to angling under certain environmental conditions and not others. If this is the case, then the evolutionary outcomes of angling selection could differ greatly between water bodies, or even within water bodies at different times, depending on the environmental conditions present in that system. Therefore, there is a critical need to better define the factors that influence angling vulnerability and, in particular, how these factors change across contexts to successfully predict the evolutionary consequences of angling.

To address this knowledge gap, the goal of this study was to identify how behavioral phenotype and food availability interact to drive vulnerability to angling of individual largemouth bass (*Micropterus salmoides*). To accomplish this goal, the behavioral phenotypes of individual largemouth bass were first determined by a series of behavior assays targeting two different axes of behavior (boldness and exploration). Following this, angling sessions were carried out in ponds with and without prey fish. Largemouth bass were chosen as the study organism for this experiment as they are a piscivorous top predator in many aquatic ecosystems, and are one of the most popular sport fish in the United States (U.S. Department of the Interior, U.S. Fish and Wildlife Service and Bureau, 2016). In addition, largemouth bass have been introduced to many locations around the world (Takamura, 2007; Taylor et al., 2019), typically to generate angling opportunities (Welcomme, 1992), making them a relevant study species. It was predicted that bold, explorative individuals would be most vulnerable to angling in the pond with prey available, and due to increased hunger, both shy, non-exploratory and bold, exploratory phenotypes would be equally vulnerable to capture in the pond with no prey.

2. Materials and methods

All described procedures were approved by the University of Illinois Institutional Animal Care and Use Committee IACUC, protocol no. 17160.

2.1. Study animals

Largemouth bass ($n = 143$) were acquired from Keystone Fish Hatchery, Richmond, IL and transported to Illinois Natural History Survey (INHS) Aquatic Research Facility near Champaign, IL on 19 September 2017. These hatchery-reared fish were one year old and naïve to fishing lures at the start of the experiment. The population had been at the hatchery for about 11 generations and the brood stock was

Table 1

Summary statistics for behavior scores, size and condition of largemouth bass. Data were collected at pond draining following the conclusion of the study; $n = 126$.

| | Range | Mean \pm SD | Median |
|-------------------------------|------------|-----------------|--------|
| Initial latency to emerge (s) | 1–900 | 116 \pm 195.5 | 46 |
| Freeze duration (s) | 3–1540 | 91 \pm 181.4 | 50 |
| Re-emergence time (s) | 4–1541 | 257 \pm 258.5 | 188 |
| Approach time (s) | 15–1800 | 841 \pm 695.2 | 466 |
| Total length (mm) | 147–234 | 180 \pm 15.9 | 180 |
| Relative weight | 85.2–131.7 | 101.7 \pm 8.7 | 100.9 |

initially collected from wild populations in southern Illinois. Mean total length (TL) \pm standard deviation (SD) of fish was 180 ± 16 mm and mean relative weight, a measure of how heavy a fish is compared to a standardized ‘ideal’ weight, was 102 ± 0.1 (Table 1), based on standard weight calculations for largemouth bass (Murphy et al., 1991). This size of fish has been previously shown to be catchable by anglers in both wild populations and in angling simulation studies (Murphy et al., 1991; Hessenauer et al., 2016; Sass et al., 2018). Upon arrival at the Research Facility, all fish were divided and held among 12 circular 1,135L outdoor tanks supplied with continuous flow-through aerated water from a nearby 0.04 ha earthen pond at a rate of ~ 8 water exchanges per day. Mean water temperature during holding was 21.8 ± 2.6 °C and mean dissolved oxygen concentration was 9.2 ± 0.8 mg/L. Fish had been feed trained since a young age, and were fed Skretting high protein pellets (Tooole, Utah) *ad libitum* daily during holding at the INHS Aquatic Research Facility. Forty-eight hours after transport, all fish were implanted with passive integrated transponder (PIT) tags (10 mm length \times 2 mm diameter, HPT12, Biomark Inc., Boise, Idaho) for individual identification. Fish were allowed to acclimate to holding conditions for 3 additional days before behavior assays began on 25 September 2017.

2.2. Behavior assays

A total of 143 largemouth bass were randomly selected for behavior assays. Prior to behavior assays, fish were moved from outdoor tanks to indoor aquaria to acclimate to lab conditions for 17–23 h, during which time no feeding occurred. Indoor aquaria (121L opaque plastic holding tanks) were each divided by an opaque plastic barrier with holes to allow for water flow between two chambers. Each aquarium held 2 fish, one on either side of the barrier to minimize interactions between individuals. A re-circulating supply of aerated water was provided via a pump from a reservoir tank equipped with an aerator (Outdoor air pump, Pentair, Cary, North Carolina). The temperature in the indoor aquaria was maintained between 23 and 24 °C with a TK 500 Heater-Chiller (Teco, Revenna, Italy) and dissolved oxygen concentrations remained above 8.0 mg/L, verified with a dissolved oxygen probe (YSI Inc. Professional Plus, Yellow Springs, OH).

Behavior assays were conducted from 25 September 2017 to 5 October 2017 and between 0830 and 1430 h in one of four identical arenas. Arenas consisted of a 180×65 cm opaque rectangular tank filled with water to a depth of 35 cm (410L). A video camera (GoPro Hero 3 or Session 4, San Mateo, California) suspended above the arena from a PVC frame was used to record fish location and behavior. The arena had a refuge zone and an open zone that were separated by an opaque 6 mm -thick Plexiglas divider. The refuge zone occupied about a quarter of the tank and had a natural gravel bottom with plastic aquarium plants for shelter, and the open zone was the remaining three-quarters of the tank and had no bottom substrate or vegetation, similar to behavioral arenas used in previous studies (Dingemanse et al., 2012; Killen et al., 2012; Fig. A1).

Immediately before behavior assays commenced, largemouth bass were netted from indoor aquaria and placed into the refuge zone of an

arena and left to acclimate for 10-min. An acclimation time of ~10 min is common for behavior assays (Vainikka et al., 2016; Louison et al., 2017), and preliminary trials revealed that largemouth bass typically began slowly moving around the refuge zone within 5–6 min after transfer. Following the 10-min acclimation period and immediately after video cameras began recording, the divider was removed using an overhead pulley system, allowing fish to emerge from the refuge zone and explore the open zone, similar to behavior assays from other studies (Jenjan et al., 2013; Louison et al., 2017). After a 15-min period where fish were allowed to explore the arena, a simulated predator attack was imposed. For this, a model great blue heron, (*Ardea herodias*) measuring 73.7 cm in height was used (United Aquatics LLC, Marlton, New Jersey), as great blue herons are a common predator of largemouth bass and have been used as simulated predators in other behavior studies with fish (Cooke et al., 2003; Bell and Stamps, 2004). For the simulated predator attack, an observer held the heron model over the behavioral arena and struck the water four times in a square pattern at the far end opposite the refuge with the heron's beak. The location of the heron strikes was the same across trials and did not vary with the position of the fish within the arena. After striking the water, the observer placed the entire heron model into the arena at the end opposite the refuge for 30 min (Huntingford and Wright, 1993; Godin and Crossman, 1994; Fedele, 2017), during which time fish location continued to be monitored. No feeding occurred in the behavior assay tanks. Following this 30-min period, the behavior assay was considered complete, video recording stopped and all fish were returned to the outdoor tank system to continue feeding until being divided and stocked into pond treatments prior to the start of angling trials (see below). Each fish was tested only once for behaviors because previous studies using similar arenas have shown these behaviors to be repeatable (Bell et al., 2009; Hart et al., 2009; Kortet et al., 2014; Mazué et al., 2015), including past work with largemouth bass where intra-class correlation coefficient values between 0.50 and 0.75 were reported for boldness behaviors (Ballew et al., 2017). In addition, repeated tests were avoided because they can encourage habituation (Réale et al., 2007), and angling vulnerability has previously been shown to be heritable for largemouth bass (Philipp et al., 2009).

Four metrics were used to score fish behavior observed in the arena: 1) latency to emerge from the refuge after the divider was initially raised (termed 'initial latency to emerge'), 2) duration of the 'freeze response' behavior after the simulated predator attack (termed 'freeze time'), 3) latency to re-emerge from the refuge following the simulated predator attack (termed 'latency to re-emerge') and 4) time to approach the predator (termed 'approach time') (Pauli et al., 2015). Behavior prior to the simulated predator attack, initial latency to emerge, was considered to reflect a fish's exploratory tendency, while behaviors following the attack (and the imposition of risk), freeze time, re-emergence time, and approach time, were considered to reflect a fish's boldness (Réale et al., 2007). Emergence from the refuge occurred when the entire body length of the fish crossed a PVC pipe separating the refuge area from the open area of the arena (Louison et al., 2017). Nearly all largemouth bass returned to the refuge and exhibited the 'freeze response' after the simulated predator attack (Bell and Stamps, 2004); thus, 'freeze time' and 'latency to re-emerge' from the refuge post simulated predator attack were also included as behavioral metrics. Fish that did not immediately return to the refuge after the simulated predator attack ($n = 3$) were removed from further analyses. 'Freeze time' was the recorded time (seconds) between when the fish initiated the freeze behavior following the simulated predator attack until the fish moved again; a movement was deemed to have occurred when the fish completed a half-body length displacement, or performed a 90-degree lateral turn. The same behavior for 'initial latency to emerge' was used for 'latency to re-emerge'. Time to approach the predator (seconds) was determined as the time between the simulated predator attack and when the fish approached within one body length of the heron's feet. If a fish did not perform any of the expected

behaviors before the behavior assay was complete, they received the maximum scores of 900 s for the initial latency to emerge behavior and 1800 s for the freeze time, latency to re-emerge and approach behaviors (Killen et al., 2011).

2.3. Angling trials

After all sets of behavior assays were complete; largemouth bass were randomly stocked into one of two 0.04 ha ponds ($n = 70$ per pond) of the same shape and the same ~2 m depth. One pond was designated as the 'fed' pond and was stocked with approximately 8,000 fathead minnows, (*Pimphales promelas*) for forage 6 days prior to receiving largemouth bass. Fathead minnows are commonly used as prey items in predation experiments (Chivers et al., 2007; Ahrens et al., 2012), and a previous study in a laboratory setting showed that largemouth bass prey on fathead minnows almost immediately once presented with them (Midway et al., 2017). The second pond was designated as the 'fasted' pond and had no fathead minnows. Both experimental ponds were drained to allow for sediment to air-dry for 7 days before refilling and fish stocking, thereby minimizing the abundance of aquatic plants and benthic invertebrates. Ponds were then refilled, stocked with fathead minnows and/or largemouth bass, and angling began one week later. As such, submerged and emergent vegetation was minimal and, although not specifically quantified, vegetative cover was similar across the ponds. Both dissolved oxygen (6.3 ± 1.3 mg/l and 7.0 ± 0.7 mg/L, for the fed and fasted pond, respectively) and temperature (17.6 ± 1.4 °C and 17.3 ± 1.4 °C for the fed and fasted pond, respectively) (YSI Inc., Professional Plus, Yellow Springs, OH) were similar across the two ponds (Welch's two sample t-tests; $p_{DO} > 0.05$; $p_{temperature} > 0.05$). Turbidity, measured as Secchi depth, was 161.1 ± 3.1 cm and 133.1 ± 17.5 cm in the fed and fasted pond, respectively, and deemed statistically different between ponds (Welch's two sample t-test; $p = 0.03$). Despite this difference, we feel that the impacts of turbidity on lure striking were unlikely as past work has shown that foraging efficiency in largemouth bass declines only when Secchi depths reach 'extreme' values, less than approximately 15 cm (Reid et al., 1999; Shoup and Wahl, 2009). The stocked largemouth bass remained in these ponds for a total of 15 days, with 7 days for acclimation and 8 days of angling. This period of food deprivation in the fasted pond is long in duration compared to some previous fasting studies that withheld food for only 6–7 days (Pettersson and Brönmark, 1993; Killen et al., 2011; Fedele, 2017).

Daily angling sessions began on 13 October 2017 and continued for 8 consecutive days. Each daily session consisted of 30-min of angling in each pond, including handling time for all captured fish. All sessions took place between 0900 and 1000 h and were completed by the same experienced angler each day. The order in which ponds were fished alternated each day. Angling gear consisted of a medium-action spinning rod and reel spooled with clear, 2.7 kg test monofilament fishing line. Two lures were used: a 2 g orange jig baited with a 5 cm pumpkinseed colored plastic grub and a size 0 Aglia in-line spinnerbait, both of which are appropriately sized for the capture of largemouth bass of the size used in this study. The jig + grub lure was used for all sessions across both treatments during the first four days of angling, and the spinnerbait was used for all sessions across both treatments during the last four days of angling. Different lure types were used to maximize catch rates because fish with different behavioral phenotypes may prefer to strike different types of lures (Wilson et al., 2015), and the lure types used here include two presentation speeds (the plastic grub is retrieved slowly, several cm below the water's surface and the spinnerbait is retrieved quickly, very close to the water's surface). During angling sessions, the angler was free to move around the pond during the sessions, casted from all areas around the perimeter of the ponds and attempted to pass the lure through all areas of the pond, thereby ensuring that all fish would be presented with the lure. Upon capture, each largemouth bass was identified by PIT tag before being released

Table 2
Spearman correlations matrix showing relationships between predictor variables of capture for largemouth bass.*.

| | Initial latency to emerge (s) | Freeze time (s) | Re-emergence time (s) | Approach time (s) | Relative weight | Total length (mm) |
|-------------------------------|-------------------------------|-----------------|-----------------------|-------------------|-----------------|-------------------|
| Initial latency to emerge (s) | – | 0.13 | –0.05 | –0.16 | 0.06 | 0.01 |
| Freeze time (s) | 0.15 | – | 0.26 | –0.01 | 0.02 | –0.03 |
| Re-emergence time (s) | 0.60 | 0.002 | – | 0.35 | 0.00 | 0.04 |
| Approach time (s) | 0.08 | 0.95 | < 0.001 | – | –0.07 | –0.08 |
| Relative weight | 0.50 | 0.81 | 0.96 | 0.41 | – | 0.21 |
| Total length (mm) | 0.92 | 0.71 | 0.62 | 0.39 | 0.02 | – |

* Correlation coefficients (r) between pairs of predictors are given in the top right section of the table and p-values for correlations are shown in the bottom left section. Significant correlations between predictors (p-values < 0.05) are shown in bold text.

back into the pond in less than one minute; no bleeding or other injury was noted for any captured fish. At the conclusion of the angling trials, ponds were drained and 63 live fish were recovered from each of the fed and fasted ponds (N = 126 total), and TL (mm) and mass (g) was recorded for each fish. Fish that were found dead or were not recovered during pond draining and therefore presumed dead, were excluded from subsequent analyses.

2.4. Data analysis

Principal components analysis (PCA) could not be used to simplify behavior metrics because the Kaiser-Meyer-Olkin test value was < 0.6, deeming PCA inappropriate (Budaev, 2010). Rather, one Spearman correlation matrix was first used to identify correlated behavioral responses with the “Hmisc” package (Table 2) (Harrell, 2019; Zuur et al., 2010). Freeze time and latency to re-emerge, latency to re-emerge and approach time and TL and relative weight were significantly correlated precluding the use of all variables in common models (Table 2). Freeze time was therefore selected for use in models below from among these correlated variables because it maximized model fit compared to other correlated metrics and because latency to re-emerge and approach time were simply reflections of freeze time (Zuur et al., 2010). Neither TL nor relative weight were related to behavioral metrics (p > 0.39 for all relationships; Table 2), and we chose to leave both TL and relative weight in our models predicting capture, even though they were correlated, because fish length is a proxy for factors such as gape size and swimming ability, which can influence capture (Dorner and Wagner, 2003; Ojanguren and Brana, 2003), and relative weight is a metric defining fish condition (i.e., low relative weight can indicate lack of food), which can also influence capture probability (Henson, 1991; Neumann et al., 2012). Spearman correlations were used to quantify whether TL and body condition (relative weight) were related to boldness.

Prior to additional statistical analysis, Welch two-sample t-tests were used to discern potential differences in TL and measured behaviors of largemouth bass between the fed and fasted ponds. Following this, a logistic regression model was used to define the factors that predicted capture during angling trials. The dependent variable for the full generalized linear model with binomial distribution was capture during angling trials (yes or no), and predictor variables were initial latency to emerge, freeze time, feeding treatment, relative weight and TL. Two-way interactions included feeding treatment × initial latency to emerge, feeding treatment × freeze time, TL × initial latency to emerge and TL × freeze time. These interactions were chosen because the goal of the study was to identify potential interactions between behavioral phenotypes and feeding treatments, and TL is known to be a predictor of angling capture. Total length and relative weight were selected for use in the models because these individual factors have been associated with exploratory and boldness behaviors (Krause et al., 1998) and can therefore potentially influence angling vulnerability; feeding treatment was included as per the goal of the study. Then, one model comparison approach based on permutations of the logistic regression models was used to compare all possible combinations of these

predictor variables and all two-way interactions against the null model, with top models ranked based on the Akaike Information Criterion adjusted for small sample sizes (AIC_c) with the “MuMin” package (Barton, 2017). Model weight was calculated for every possible combination of fixed effects and included interactions, with the top models being the ones with the highest model weights. Full-model averaging, the use of all possible combinations of predictor variables in models, was then used to determine the predictor variables with the greatest influences on whether a fish was captured by using the “MuMin” package (Arnold, 2010; Barton, 2017; Symonds and Moussalli, 2011). Full-model averaging was used in place of natural model averaging because of high model selection uncertainty, with no models producing model weights > 0.90 (Symonds and Moussalli, 2011). Model comparison was used for the logistic regression because there were many predictor variables included in these models, and the goal of this statistical test was to discern the relative influence of each predictor variable in relation to capture vulnerability. For this, the sum of the Akaike weights for each parameter included in all the models where they appeared were calculated to quantify relative importance (Arnold, 2010; Symonds and Moussalli, 2011). Relative importance values close to one represent predictors that strongly influence fish capture and low relative importance values, those close to zero, represent predictors that have little influence on capture (Arnold, 2010). To explicitly quantify how predictor variables influenced captures (including recaptures) across the different angling sessions (time), a multi-event Cox regression was conducted using the same predictor variables used in the full generalized linear model described above (Amorim and Cai, 2015).

One Poisson regression was used to compare the total number of captures between ponds across the 8 angling sessions and whether catch rates within each session were different between the fed and fasted ponds. This regression model included the number of captures as the dependent variable (a count), with feeding treatment, session number (nested within lure type) and their interaction as fixed effects. For the Poisson, only one model was used to discern factors affecting the total number of captures because the goal was to see how each variable affected capture. Variance inflation factor (VIF) scores were used to identify possible collinearity between variables within the Poisson model. All VIF scores were less than 6, indicating that variables within the Poisson model are not collinear, as scores below 10 indicate that variables are independent (Table A1; O'Brien, 2007). Additionally, VIF scores for categorical variables (as we have) should be interpreted cautiously (Murray et al., 2012), and biological knowledge of the study system and questions being asked should also be taken into account when generating models and making decisions related to including or excluding variables in models (Zuur et al., 2010). Session was nested within lure type to account for a possible change in catch rate starting with session 5, resulting from switching to a lure that was unfamiliar to the fish (Lennox et al., 2017; Louison et al., 2019). The full model was used without model selection. Due to overdispersion, defined as residual deviance larger than the residual degrees of freedom (Crawley, 2013), a negative binomial model was used, which accommodates for over-dispersion in count data regressions, within R package “glmmADMB” (Fournier et al., 2012; Zeileis et al., 2008).

Table 3
Top 10, null and full logistic regression models for largemouth bass capture during experimental angling trials.^a

| Model | AIC _C | ΔAIC _C | -2 log likelihood | W _i |
|---|------------------|-------------------|-------------------|----------------|
| Total length + feeding treatment | 127.86 | 0.00 | 121.67 | 0.10 |
| Total length + feeding treatment + freeze + relative weight | 128.90 | 1.03 | 120.57 | 0.06 |
| Total length | 129.00 | 1.14 | 121.68 | 0.06 |
| Total length + initial latency to emerge + feeding treatment + total length × initial latency to emerge | 129.10 | 1.23 | 118.60 | 0.06 |
| Total length + feeding treatment + freeze | 129.50 | 1.64 | 121.17 | 0.05 |
| Total length + initial latency to emerge + total length × initial latency to emerge | 129.65 | 1.79 | 121.32 | 0.04 |
| Total length + initial latency to emerge + feeding treatment | 129.68 | 1.18 | 121.35 | 0.04 |
| Total length + relative weight | 130.10 | 2.23 | 123.90 | 0.03 |
| Total length + initial latency to emerge + feeding treatment + relative weight + total length × initial latency to emerge | 130.22 | 2.36 | 117.52 | 0.03 |
| Total length + freeze | 130.59 | 2.72 | 124.39 | 0.03 |
| Null model | 140.35 | 12.48 | 138.32 | 0.0002 |
| Full model: Total length + initial latency to emerge + feeding treatment + freeze + relative weight + total length × initial latency to emerge + total length × freeze + initial latency to emerge × feeding treatment + freeze × feeding treatment | 137.79 | 9.93 | 115.88 | 0.0007 |

^a Sample size was 126 individuals. W_i is model weight.

For the 10 models with the lowest ΔAIC scores, individual model fit was assessed via visual examination of Pearson residuals (i.e., quantile-quantile plots to define normality of residuals by predicted plots to define homogeneity of variances), as well as an inspection of outlier observations (Table 3), with the “car” package (Fox and Weisberg, 2011; Menard, 2002; Zhang, 2016). Results from the model fit analyses, as well as outlier analyses, indicated the absence of influential data points or outliers, so all data were included in the statistical models. Given uneven sample sizes of captured and uncaptured largemouth bass (see results below), a power analysis was completed for both exploratory and boldness behaviors to predict capture vulnerability in statistical models ($\alpha = 0.10$ for one-sided behavior distributions), with the “powerMediation” package (Qiu, 2018). All figures were made through the use of the “ggplot2” and “gridExtra” packages (Auguie, 2017; Wickham, 2009). All analyses were conducted in R version 3.4.1 (R Core Team, Vienna, Austria); the significance level (α) was set at 0.05.

3. Results

During behavior assays to determine behavioral phenotype of each individual, the time required for largemouth bass to initially emerge from the refuge averaged approximately 116 ± 195.5 s (Table 1). Once in the refuge after the simulated predator attack, largemouth bass remained motionless for approximately 91 ± 181 s, returned to the open zone after approximately 257 ± 258 s and required, on average, 841 ± 695 s to approach the heron model (Table 1, Fig. A2). The variation of individual fish behavior in these data are similar to the behavioral ranges found in previous studies that used similar protocols for behavioral assays of this kind (Killen et al., 2011, 2012).

Seventy largemouth bass were initially stocked into each pond; TL \pm SD did not differ between ponds (TL_{fed} = 176 ± 17 mm, TL_{fasted} = 175 ± 15 mm; Welch two-sample t-test, $t_{134.86} = 0.61$, $p = 0.541$). In addition, initial latency to emerge and freeze times did not differ significantly between the fed and fasted ponds (mean initial latency to emerge in fasted pond = 110.7 ± 185.7 s, mean initial latency to emerge in fed pond = 122.2 ± 206.1 s, Welch two sample t-test, $t_{122.22} = -0.33$, $p = 0.741$; mean freeze time for fasted pond = 105.0 ± 220.1 s, mean freeze time in fed pond = 76.4 ± 132.3 s, Welch two sample t-test, $t_{101.64} = 0.88$, $p = 0.379$; Fig. 1a and b).

At the conclusion of the angling trials, 14 fish were captured from the fed pond (20 % of individuals stocked), with 12 fish captured once and two fish captured twice. Twenty-three fish were captured from the fasted pond (33 % of individuals stocked), with 19 fish captured once and four captured twice. Seven models relating the effects of behavioral metrics and experimental treatments on capture probability had ΔAIC_C values < 2 and all had ΔAIC_C values lower than either the full model with all possible predictor variables or the null model (Table 3). The

strongest variable predicting fish capture was total length with a relative importance of 1.00. This finding indicates larger fish were more likely to be captured than smaller fish, despite the fact that mean lengths of captured and uncaptured fish differed by only 12 mm (Fig. 1c). Feeding treatment was the second strongest predictor of fish capture, with a relative importance value of 0.69, indicating that fish in the fasted pond were more likely to be captured than were fish in the fed pond. Initial latency to emerge, freeze time, and relative weight had smaller relative importance values at 0.55, 0.42 and 0.36, respectively. Power analysis supported weak contributions of initial latency to emerge and freeze time to impact capture, with power values of 0.05 and 0.06, respectively. Therefore, either the influence of these behaviors to predict capture was indeed weak, or the ability to detect significant effects based on the number of fish captured was small. However, the sample size of largemouth bass assayed in the laboratory and captured during angling trials was similar to previous studies linking behavior to vulnerability (Table A3). The two-way interaction with the greatest influence on capture likelihood was total length × initial latency to emerge, with a relative importance of 0.31 and the two-way interactions feeding treatment × initial latency to emerge and feeding treatment × freeze time had weaker influences on capture likelihood, with relative importance values of 0.11 and 0.09, respectively. The outcome of the multi-event Cox regression quantifying the effects of different factors on time to capture was identical to that of the full generalized linear model, with total length being the only significant predictor variable influencing capture probability of both the initial and repeat captures across angling sessions, such that larger fish were more likely to be captured sooner than smaller individuals (Table A4).

Overall, for both fed and fasted ponds, there was a significant negative relationship between number of fish captured and angling session, with the highest number of fish captured at the start of the angling trials and capture rates decreasing thereafter (Table 4; Fig. 2). While the total number of captures across all angling sessions did not differ by feeding treatment alone, the interaction between treatment and session (nested within lure type) was a significant factor predicting the number of fish captured (Table 4). This interaction resulted from catch rates in the fasted pond remaining higher into later sessions than catch rates in the fed pond, which remained low (Fig. 2). Additionally, catch rates increased in session 5 in the fasted pond immediately after the lure switch but remained relatively low in the fed pond.

4. Discussion

Fish capture by recreational anglers requires the intersection of a number of factors that include spatial overlap of angler and fish, coupled with an interest or willingness of a fish to strike a lure (Lennox et al., 2017). Past work with carp and trout species has shown that fish behavior can influence the likelihood of capture, with bold, active

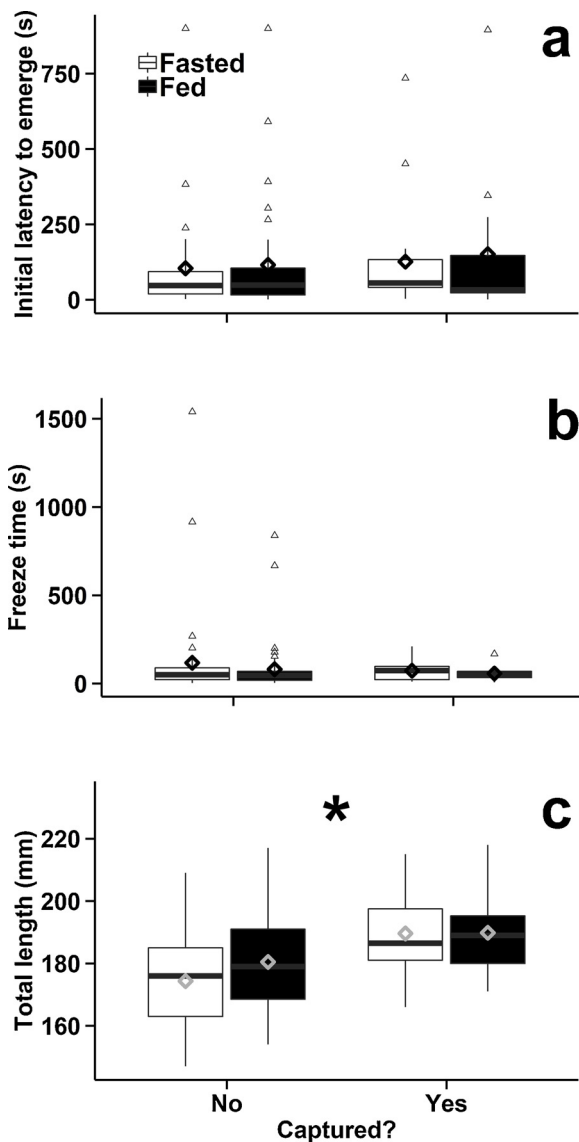


Fig. 1. Total length and behavioral traits as predictors of capture. Boxplots of (a) initial latency to emerge (seconds) (b) freeze time (seconds), and (c) total length (mm) for largemouth bass captured and not captured during experimental angling trials. Asterisk denotes a significant ($p < 0.05$) difference between captured and uncaptured fish. The lines in the boxes are the median, diamonds are the mean, whiskers represent the upper and lower quartiles \pm the interquartile range, and open triangles are outliers that fall outside if the interquartile range (below 25th percentile or above 75th percentile).

Table 4

Model output for negative binomial Poisson regression with the total number of captures of largemouth bass as the dependent variable and feeding treatment, lure type nested within angling session and their interactions as fixed effects.*.

| | Parameter Estimate | SE | z-score | p |
|---|--------------------|-------------|-------------|--------------|
| Angling session | -0.92 | 0.33 | -2.83 | 0.005 |
| Feeding treatment | 1.04 | 1.02 | 1.02 | 0.31 |
| Feeding treatment \times angling session | -0.95 | 0.75 | -1.28 | 0.20 |
| Fasted treatment \times angling session (lure type) | 0.60 | 0.26 | 2.32 | 0.02 |
| Fed treatment \times angling session (lure type) | 1.21 | 0.55 | 2.20 | 0.03 |

* Significant predictors of capture within angling sessions ($p < 0.05$) are shown in bold text.

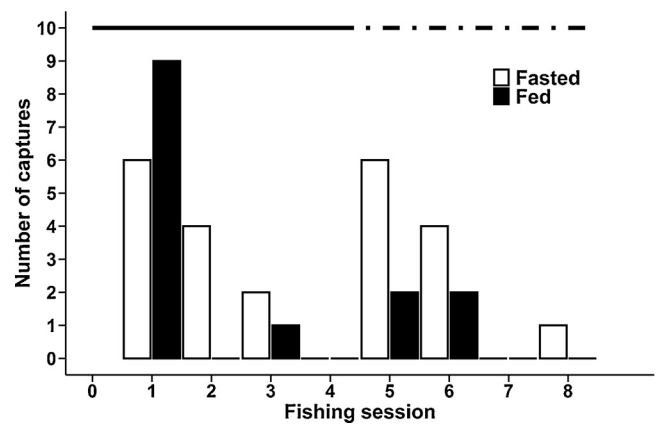


Fig. 2. Captures across fishing sessions. Number of unique individual large-mouth bass captured across eight angling sessions in fasted and fed ponds. Lures were changed after fishing session 4. The jig + grub lure was used during fishing sessions 1–4, with capture bars under the solid line, and the spinnerbait lure was used during fishing sessions 5–8, with capture bars under the dashed line.

individuals more often captured relative to shy, sedentary fish (Arlinghaus et al., 2017; Biro and Post, 2008; Klefoth et al., 2017). As a result, it is possible that these bold, active individuals could be disproportionately removed from the population through harvest, which, in turn, could lead to a predominance of timid, inactive fish, and a host of negative consequences for a population (Arlinghaus et al., 2017). Results from the current study with largemouth bass, a sit-and-wait predator (Demers et al., 1996), suggest that angling pressure may not be a force of behavioral selection for this species, as indices of boldness and exploration did not influence the likelihood of capture, even across varying prey densities. However, other aspects of the timidity syndrome, including angler avoidance, fish-angler spatial overlap, and other behaviors may still be at play during largemouth bass angling events (Arlinghaus et al., 2017). Results from this study, along with others in the literature, suggest that largemouth bass capture is more heavily influenced by size (current study), stress hormone responsiveness (Louison et al., 2017), prior experience with angling (Louison et al., 2019), and possibly learning (current study; Wegener et al., 2018) upon encountering a lure. As such, there is little evidence to suggest that angling or harvest will alter the relative abundance of bold, exploratory largemouth bass in a population.

Behavioral phenotype was not a strong predictor of capture for largemouth bass, with behavioral phenotypes equally likely to be captured in both feeding treatments, and across the different angling sessions. The relative importance of initial latency to emerge, a measure of exploration, and freeze time, a measure of boldness, in the model predicting angling vulnerability were 0.55 and 0.42, respectively, indicating only weak links between lab-measured behaviors and angling vulnerability. These weak links were also confirmed through a power analysis, which suggested that behaviors would not have predicted angling vulnerability within the sample sizes used, even under sufficient power. Several studies have linked behavioral phenotypes and correlated metabolic rates with angling vulnerability (Biro and Post, 2008; Biro and Sampson, 2015; Lennox et al., 2017; Mittelbach et al., 2014; Wilson et al., 1993), though this conclusion has not been consistent. For example, studies with rainbow trout (Biro and Post, 2008) and brown trout, *Salmo trutta* (Härkönen et al., 2014) found that bold fish exhibiting high exploration rates were more susceptible to angling relative to shy fish with low exploration rates. The lack of a relationship between behavioral phenotype and capture rates in the current study may be due to species-specific differences between largemouth bass and other fish examined previously. More specifically, largemouth bass have been identified as sit-and-wait predators (Demers et al., 1996),

and behavioral metrics related to exploration may not factor into their foraging style or interaction with lures (Lennox et al., 2017). Indeed, Louison et al. (2017) found that laboratory-based boldness behaviors did not predict angling vulnerability for largemouth bass, noting that capture was better predicted by stress hormone responsiveness. The traditional framework built around angling vulnerability has been based off of carp and trout species, which have more active foraging and movement ecology, and therefore activity rates may have stronger relationships with the likelihood of these fish species to encounter fishing lures, providing a stronger link between foraging activities and angling vulnerability (Lennox et al., 2017). Finally, behaviors are often reflections of immediate environmental stimuli, and the stimuli presented to largemouth bass in the behavioral arena likely differed from stimuli in ponds, such that laboratory-derived behaviors may not carry over into field situations (Toms et al., 2010). Data from this study show that boldness and exploratory behavioral phenotypes are not drivers of angling vulnerability for largemouth bass.

In contrast to expectations, food availability did not impact which behavioral phenotype was most vulnerable to angling. The relative importance values of the interactions between behavioral metrics and feeding treatment to predict capture were weak, and these interactions were not significant factors in time series model, indicating that behavioral phenotypes were captured at similar rates across feeding treatments. Previous studies have documented behavioral changes across environmental contexts (Pettersson and Brönmark, 1993; Naslund and Johnsson, 2016), including a study by Beukema (1968) who found that hungry three-spined sticklebacks (*Gasterosteus aculeatus*), had higher rates of activity and prey encounters while foraging. Results from the current study clearly show that food availability did not affect which behavioral phenotypes were captured by anglers.

Feeding treatment had an impact on catch rates, with largemouth bass from the pond with no minnows more likely to be captured than fish from the pond with minnows. Several past studies have also found that food availability can influence capture rate, with anglers more likely to have higher capture rates of walleyes (*Sander vitreus*) when abundance of prey was low (VanDeValk et al., 2005). However, this conclusion is not universal, as Fedele (2017) found that food availability for juvenile rock bass, (*Ambloplites rupestris*), had no effect on capture. Past studies would suggest that low prey densities should result in elevated capture rates by anglers as reduced food availability can lead to more explorative behaviors (Beukema, 1968; Härkönen et al., 2014), presumably as fish engage in energy-acquisition behaviors (Klefoth et al., 2017; Pettersson and Brönmark, 1993). However, largemouth bass are largely sit-and-wait predators that wait for food to come to them (Demers et al., 1996). Gingerich et al. (2010) showed that food deprivation in largemouth bass reduces metabolic rate, likely to conserve energy, and recent laboratory work by Keiling and Suski (2019) showed that food deprivation actually reduced activity levels in largemouth bass, so exploration and foraging do not appear to be elevated following food deprivation in this species. In addition, work by Keiling and Suski (2019) demonstrated that food deprivation did not increase novel object inspection behaviors in largemouth bass, suggesting that boldness levels did not increase with food deprivation. Capture rates in the pond with no minnows may have, therefore, been elevated due to an increased likelihood of fish to strike and/or ingest lures (Lennox et al., 2017), an increase in aggression or territoriality upon being presented with a lure (Suski and Philipp, 2004), or other elements of stress that occur during food deprivation not currently quantified. However, we were not able to quantify potential differences in activity rate or other behavioral metrics for fish while in experimental ponds, and so cannot relate prey availability to movement; exploring this relationship in more detail would be an avenue for future research. Together, the number of largemouth bass captured was higher in the pond with no minnows compared to the pond with minnows, a relationship between food availability and capture that was found in other studies, as well (Bryan, 1974; Heermann et al., 2013; Lennox

et al., 2017).

Across both the fed and fasted treatments, fish size was the strongest predictor of capture, with larger fish more likely to strike lures than smaller fish, even with a relatively small mean difference in length between captured and uncaptured fish; these differences in capture rate across sizes were consistent across the different angling sessions. Previous studies have supported the positive relationship between total length of fish and capture probability (Biro and Post, 2008; Klefoth et al., 2017; Monk and Arlinghaus, 2018), and there are a number of possible explanations for why larger fish were more likely to strike lures in the current study. For example, work by Suski and Philipp (2004) showed that, during the brood guarding period, larger nesting males were more active and intense at guarding their offspring than were smaller nesting males. At present, it is not known if larger fish are more aggressive than smaller fish outside of the brood-guarding period, or for males versus females, but variation in aggression could be an explanation for why larger fish were disproportionately captured relative to smaller fish, and should be the subject of future study. Additionally, previous studies have found fish in exploited populations have lower metabolic rates than unfished populations, suggesting that the fish with high metabolic rates were vulnerable to angling and were removed from these systems (Hessenauer et al., 2015; Redpath et al., 2010). Larger fish may also be behaviorally dominant and less fearful of novel lures than smaller fish, leading to large fish outcompeting small fish to strike fishing lures (Krause, 1994). It should be noted that the mean size of largemouth bass used in this study (180 mm) falls below the minimum total length threshold for capture of 200 mm seen in some studies (Wegener et al., 2018), but is still within the range of sizes captured in other studies (Anderson and Heman, 1969; Nannini et al., 2011). As fish size and relative weight were correlated, it is also important to note that any artificial selection that may affect fish size may also affect relative weight within exploited populations. Turbidity may have influenced capture vulnerability, because the fasted pond was more turbid than the fed pond, and this increased turbidity may have minimized opportunities for the largemouth bass to inspect lures (and decipher lures from food sources), leading to more lure-striking and captures. However, turbidity in both ponds was well below levels that are expected to affect foraging behaviors and success (Reid et al., 1999; Shoup and Wahl, 2009). Owing to the fact that the hatchery-reared fish used here may be bolder and more active than wild fish (Biro and Post, 2008), future studies using largemouth bass across a greater range of sizes, and from wild populations that have not received supplemental hatchery stocking, should be useful to further explore relationships between fish size, behavioral phenotypes and angling vulnerability. Data from the current study show that larger largemouth bass were more likely to be captured over smaller conspecifics, regardless of feeding treatments.

Capture rates declined over angling sessions in both the fed and fasted treatments. The largest number of captures for both fed and fasted treatments was in angling session one and the number of captures declined in each session until session 5 after lures were changed, when the decline was repeated. Declines in hook-and-line capture rates over time have been demonstrated many times and across multiple species (VanDeValk et al., 2005; Askey et al., 2006; Hessenauer et al., 2016). For example, highly vulnerable rainbow trout avoided fishing lures after about 10 days (Askey et al., 2006), while catch rates of largemouth bass in an experimental pond also declined over time (Hessenauer et al., 2016). There are a number of reasons why capture rates of fishes can decline over time, including reductions in population density due to harvest (VanDeValk et al., 2005) and shifts toward more timid phenotypes in exploited populations as bold individuals are harvested, known as the timidity-syndrome (Arlinghaus et al., 2017). The timidity-syndrome occurs when fish populations experience long-term fishing exploitation, increasing the “landscape of fear” effect, leading to lower activity rates, lower exploration, and lower willingness to approach and ingest fishing lures (Arlinghaus et al., 2017). More

importantly, because behaviors have a genetic component, the effects of long-term disproportionate harvest can be more concrete and alter mean population behaviors on a genotypic level (Arlinghaus et al., 2017). However, these explanations likely do not apply to the largemouth bass in the current study as captured fish were returned to the pond keeping density constant, and we did not see any influence of behavior on capture likelihood. Learning to avoid hooks is also common in fisheries and has previously been identified as a factor contributing to catch rate declines over time (Fedele, 2017; Fernö and Huse, 1983; Laugen et al., 2014; Lennox et al., 2016). Additionally, largemouth bass can exhibit “angler avoidance” to negative stimuli including the presence of boats and people, independent of lures and capture, where the catch rate of fish in small impoundments declined over a 6-month period when a total of 11 fishing lure types were used with the absence of harvest (Wegener et al., 2018). Regardless of the mechanism, the current study showed a decline in capture rate of largemouth bass across successive angling sessions.

Despite the clear findings of this study, there are a number of avenues for future work, as well as some potential caveats, to further develop mechanisms of angling vulnerability and their evolutionary consequences (Lennox et al., 2017). For example, fish have previously been found to demonstrate five behavioral axes: boldness, exploration, sociability, activity and aggression (Conrad et al., 2011; Réale et al., 2007). In the current study, we examined the role of only two behavioral axes (exploration and boldness), and additional work exploring the other three axes should be performed to enhance our understanding of angling vulnerability. In particular, aggression, (defined as a reaction to nearby conspecifics and/or defense of a territory (Koolhaas, 2008; Reale et al., 2010; Sloman, 2011) should be examined, as there may be a potential for this axis to influence capture, but work with this axis has been limited and constrained. More specifically, past work has shown that male largemouth bass that are more aggressive (defined as more intense defense of broods and/or nests) are more vulnerable to hook-and-line capture (Suski and Philipp, 2004; Sutter et al., 2012). However, aggression and lure striking in nesting male bass is complicated by the fact that both correlate positively with individual size and brood size, such that larger (older) males obtain more eggs than smaller males, defend them more aggressively and are more likely to strike lures, making it difficult to tease apart the effects of size/age, potential fitness and response to predators (Suski and Philipp, 2004; Sutter et al., 2012). Clearly, angling during the brood guarding period has the potential to remove large, aggressive males with the greatest fitness potential, and future work with largemouth bass should follow up on this finding to quantify aggression and lure striking more explicitly, particularly focusing on non-nesting periods, and including both males and females in analyses. Similarly, we limited our study to two different lures, but studies have shown that fish vary in the way that they approach and ingest lures of different sizes (Gutowsky et al., 2017), highlighting the need to consider how different lure types can influence capture and harvest. Finally, capture is only possible when anglers encounter fish (Lennox et al., 2017), and so factors driving the spatial and temporal distributions of both anglers and fish should be quantified to define capture likelihood (Matthias et al., 2014). This work, as well as numerous other potential factors, can be explored in both a controlled setting similar to the current study, or with a lab study, ensuring that issues of replication, adequate sample sizes, and control of environmental variables has occurred to increase the confidence in results.

5. Conclusions

Findings from this study have three main implications for the ecology and management of recreational fish populations. First, results suggest that angler-induced changes to the boldness and exploratory behaviors of largemouth bass are not likely as different behavioral phenotypes were captured at similar rates, regardless of food

availability. This finding establishes a new framework to explain capture in largemouth bass in that capture does not appear to be influenced by boldness or exploration, and is due to factors such as size and learning, coupled with stress responsiveness (Louison et al., 2017). Second, results suggest that the largest, fastest-growing largemouth bass can be disproportionately removed from aquatic systems through harvest. Over time, this selective removal of fast-growing individuals could lead to declines in both catch rates and angler satisfaction as growth rates (and therefore size) and behavioral traits such as exploration are often correlated (Alós et al., 2016; Arlinghaus et al., 2017). Finally, because fish in ponds with low prey abundance were more vulnerable to capture, environmental factors, such as prey abundance, must be considered when managing populations of largemouth bass. While one aspect of angler satisfaction relates to the size of fish captured (Dotson et al., 2013), another aspect of angler satisfaction relates to catch rates and the capture of large numbers of fish (Young and Hayes, 2004), which is likely to occur in systems with low prey available to the target species. Results suggest that an overabundance of prey in a system may create declines in catch rates (VanDeValk et al., 2005), suggesting that managers be aware of prey availability for largemouth bass fisheries. Obviously, if prey abundance falls too low, growth and abundance of the targeted predator species can plummet, emphasizing the need for an ideal amount of prey to be available to the predator species. To summarize, results from this study do not suggest selection against exploratory and boldness behavioral traits, but size and growth rates may be selected upon through harvest; and environmental conditions, including food availability, may alter the strength of selection. The ecological impacts of selective harvest should be considered in future management plans and policies to minimize effects of artificial selection and maintain balanced recreational fish populations.

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CRediT authorship contribution statement

Toniann D. Keiling: Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Supervision, Visualization, Writing - original draft, Writing - review & editing. **Michael J. Louison:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, Software, Writing - review & editing. **Cory D. Suski:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Resources, Software, Supervision, Validation, Visualization, Writing - review & editing.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishres.2020.105554>.

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