

MANAGEMENT BRIEF

Capture Is Predicted by Behavior and Size, Not Metabolism, in Muskellunge

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Abstract

Fish that strike angling lures often have a set of characteristics that predispose them to capture. Vulnerable fish may then be removed from a population, either through harvest or incidental mortality, and in turn leave individuals in a population that are less vulnerable to angling. Over time, the removal of vulnerable individuals can erode capture rates, possibly resulting in evolutionary changes if traits that result in capture correlate with characteristics such as fecundity or growth. We sought to define the mechanisms driving individual angling vulnerability in Muskellunge *Esox masquinongy*, with the intent of informing management activities to conserve populations. The behavior of individually identified Muskellunge ($n = 68$; mean TL = 310.2 mm; range = 229–350 mm) was assessed using standard open-field tests; the fish were then stocked into earthen-bottom ponds to assess angling vulnerability. After angling, all captured fish and a subset of uncaptured fish were assessed for metabolic parameters. Results indicated that larger Muskellunge displaying low levels of exploration and aggression were preferentially captured. Behaviors such as boldness and activity did not influence capture, and metabolic parameters did not differ between captured and uncaptured fish.

Recreational angling is a popular activity around the world (Cooke and Cowx 2006; Brownscombe et al. 2017), with five times more recreational anglers than commercial harvesters (Arlinghaus et al. 2019). Globally, billions of dollars are generated (FAO 2012) by the approximately 700 million recreational anglers that capture fish each year

(Cooke and Cowx 2004, 2006). People partake in recreational angling for a variety of reasons, including the pursuit of fish for food or achievement (e.g., capture and size of capture) and intrinsic reasons (e.g., enjoying nature; Birdsong et al. 2021), making it an economically and socially valuable activity.

Angling has the potential to influence fish populations through both direct and indirect effects (Cooke and Cowx 2006; Brownscombe et al. 2017). For example, many fisheries are subject to harvest by recreational anglers, with captured fish being consumed for food. In addition, even for situations in which an angler's goal is not to harvest fish for food, angled fish are subjected to a host of challenges, including hooking, exercise, and air exposure (Cooke and Suski 2005). In some cases, fish may experience initial or delayed mortality after angling due to the cumulative impacts of these stressors (Meka and McCormick 2005; Jørgensen and Holt 2013). The loss of individual fish from the population can accumulate and lead to decreases in population size (Post et al. 2002), which may occur even when capture rates remain high (i.e., hyperstability; Erisman et al. 2011; Ward et al. 2013).

More recently, it has been demonstrated that angling can also impart an indirect impact on fish populations by selecting for individuals with specific behavioral types that predispose an individual to capture. Briefly, animal behaviors can be categorized into five separate axes: aggression,

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boldness, activity, exploration, and sociability (Réale et al. 2007). Behavioral phenotype can be connected to aspects of an individual's physiology, such as metabolic rate, within the pace-of-life framework (Réale et al. 2007) and is in turn capable of shaping the likelihood that an individual fish will be captured by anglers. For example, in Common Carp *Cyprinus carpio*, bolder and more active individuals were captured (Klefoth et al. 2017). In Rainbow Trout *Oncorhynchus mykiss*, individuals that were more active and stress resilient were disproportionately captured (Koeck et al. 2019). Work with Largemouth Bass *Micropterus salmoides* found that individuals with a lower stress responsiveness and higher aggression during the brood-guarding stage were captured (Suski and Philipp 2004; Louison et al. 2017). In addition, Redpath et al. (2010) showed that populations of Largemouth Bass that were highly vulnerable to angling had increased metabolic rates relative to less-vulnerable conspecifics, thereby indicating a link between angling vulnerability and metabolic parameters. Behavior in fish is a heritable trait that is consistent over time (Cooke et al. 2007; Biro and Stamps 2008; Philipp et al. 2015), relating to individual fitness and reproductive success (Réale et al. 2007; Biro and Stamps 2008; Sutter et al. 2012). As a result, owing to the possible changes to either angler catch rates or population-level parameters, a reduction in angling quality is possible. It is therefore critical to define the behavioral predictors of angling so as to inform managers of possible short- and long-term changes to populations that may occur due to angler impacts.

The Muskellunge *Esox masquinongy* is an apex predator in the systems it occupies, with adult fish filling an important niche by consuming large prey items and facilitating top-down control of ecosystems (Glade 2021). Muskellunge are also popular with anglers (Fayram 2003) and are long-lived fish, with some individuals attaining ages upwards of 30 years (Casselmann and Crossman 1986). Muskellunge are historically overfished (Crossman 1986); additionally, in fisheries with warmer waters, such as more southerly latitudes or summer seasons, the risk of mortality after an angling event increases (Booth 2022; Jenkins 2022). Finally, and most importantly, Muskellunge are colloquially termed “the fish of 10,000 casts,” highlighting their wary nature and reluctance to capture, making this fish an ideal species with which to explore questions on factors that influence lure striking.

The goal of this study was to quantify the role of behavioral and physiological factors influencing the likelihood of capture in Muskellunge. To accomplish this goal, we first conducted behavioral assays using hatchery-reared Muskellunge before stocking them into earthen ponds, where they were targeted by anglers using conventional gear. A subset of uncaptured fish, along with all captured fish, was subsequently assayed for metabolic parameters.

When combined, the results from this study highlight factors that best predict angling vulnerability in Muskellunge, and our findings ultimately suggest ways in which angling may be influencing populations of Muskellunge over time.

METHODS

We obtained a total of 68 age-0 Muskellunge from the Illinois Department of Natural Resources' Jake Wolfe Memorial Fish Hatchery, Topeka, on September 11, 2021 (total weight [mean \pm SD] = 147.8 \pm 24.8 g; TL = 310.2 \pm 19.8 mm), and transported them to the Aquatic Research Facility at the University of Illinois, Urbana. The Muskellunge used in the present study are annually produced from batch crosses collected from fish netted within North Spring Lake at Manito, Illinois. Upon arrival at the aquatic facility, fish were haphazardly distributed across six 1,135-L, outdoor holding tanks connected via a flow through system to an adjacent earthen-bottom pond (dissolved oxygen = 8.8 \pm 0.7 mg/L; Professional Plus dissolved oxygen and temperature meter; YSI, Inc., Yellow Springs, Ohio). Muskellunge were held in these tanks for 48 h to acclimate. Each fish was then implanted with a PIT tag (Biomark, Boise, Idaho) within the peritoneal cavity for individual identification, a procedure that was previously shown to have high retention while not inducing negative outcomes in Muskellunge (Wagner et al. 2007). During holding, fish were fed either Golden Shiner *Notemigonus crysoleucas* (obtained from a local bait shop) or Fathead Minnow *Pimephales promelas* (obtained from I. F. Anderson Farms, Lonoke, Arkansas) ad libitum. Fish were held within the outdoor holding tanks for a minimum of 3 d before commencing behavioral assessments.

Behavior assessments.—Behavioral assessments consisted of standard “open-field” tests to quantify boldness, exploration, and aggression during a 30-min trial broken into three 10-min segments (Koolhaas et al. 1999; Réale et al. 2007). All behavior assays were conducted between 0730 and 1800 hours on September 16–20, 2021, within one of four identical indoor arenas that consisted of a 565-L, rectangular polyethylene stock tank (181 cm long \times 65 cm wide) that was filled with water to a depth of 20 cm and that was isolated on all four sides with blackout curtains to avoid external stimuli. Behavioral arenas were divided into two distinct sections: a refuge zone and an open zone. The refuge zone comprised approximately one-third of the tank area and contained gravel substrate along with one artificial aquatic plant. The refuge was separated from the remainder of the tank with a white Plexiglas divider attached to a pulley and was covered with a lid. The remaining two-thirds of the stock tank were considered the open zone, and this zone was uncovered. The end of the open zone farthest from the refuge contained a matte-gray Plexiglas divider attached to a pulley that fully

covered a 14 × 9-cm mirror mounted approximately 0.5 cm from the tank bottom in a position that was easily visible to the fish. Each arena was outfitted with a video camera (either a GoPro Hero 3 [GoPro, San Mateo, California] or a Sony Handycam CX405 [Sony, Tokyo, Japan]), which was mounted above the tank on the refuge side.

Each behavioral assay was 30 min in total, composed of three segments that were 10 min in duration and occurred seamlessly one after the other: a pre-lure exploration assessment, a lure phase that was intended to quantify the response to a novel object (a fishing lure), and a mirror phase that was intended to quantify aggression. For behavioral trials, Muskellunge were haphazardly netted from the outdoor aquaria, identified by utilizing a PIT tag reader (Biomark HPR Lite), and transferred to the refuge zone of the arena. Fish were left to acclimate within the refuge for 20 min before the start of a trial, a period of time deemed sufficient for fish to become quiescent based on pilot trials. After this acclimation period, video recording started and the barrier at the end of the refuge was lifted, permitting the fish to leave the refuge and enter the exploration zone to explore, with no external stimuli (Réale et al. 2007). During this period, behaviors that were observed included time to first emerge from the refuge (Hulthén et al. 2017; Louison et al. 2017), frequency of emerging from the refuge after a return to the refuge, time spent in the open arena (Louison et al. 2017), and duration of time spent moving while in the open arena (Wilson and Godin 2010). After 10 min of exploration, a hookless fishing lure (7.5-cm, soft-plastic bait, pearl-white color, in the shape of a minnow) was dropped into the center of the arena. The lure served as a novel object presented in a way that mimicked a fishing experience, and the response of the fish to a novel object presented in this way provides a measure of boldness, as the fish would take a risk to leave the refuge and interact near the novel object, with bolder individuals spending more time outside of the refuge (often resulting in proximity to the novel object) or transitioning between zones more (Réale et al. 2007; White et al. 2013; Näslund and Johnson 2016; Keiling and Suski 2019). During the lure phase, all of the same aforementioned behaviors were quantified, with the addition of freeze time (total time spent motionless after introduction of the lure) and a count of the number of lure inspections (Keiling and Suski 2019; Keiling et al. 2020). Ten minutes after the presentation of the lure (20 min after the start of the behavioral trial), the mirror phase of the behavioral assay began. For this phase, the Plexiglas divider at the far end of the arena was lifted to reveal a mirror—a typical method in assessing aggression (Way et al. 2015; Baran and Strelman 2020). The fish was exposed to the mirror for 10 min, during which time we quantified the same metrics that were recorded for the pre-lure phase, with the addition of counting the number

of mirror displays and quantifying the duration of time spent within one body length of the mirror (Way et al. 2015). After the mirror phase, the behavioral trial ended, the recording was stopped, and Muskellunge were returned to the outdoor holding tanks described above.

After the initial behavioral trial, Muskellunge remained in the outdoor holding tank for a minimum of 7 d (while being fed ad libitum) before undergoing for a second time the same testing procedure described above. Conducting two identical behavioral assessments of each fish allowed for the calculation of a repeatability score for behavioral metrics (Bell et al. 2009; Dingemanse and Wright 2020). The lone difference between the first and second behavioral assessments was that for the second assessment, a different fishing lure was used (a white plastic bait that mimicked a worm) to minimize habituation to the stimulus (White et al. 2013). While it is important to maximize the duration of time between replicate trials to minimize the likelihood of habituation to the testing environment (Réale et al. 2007; Dingemanse et al. 2012), a holding duration of 7 d between replicate behavioral trials in the current study minimized the potential for variation in abiotic characteristics that is inevitable when holding animals outdoors (i.e., seasonal declines in temperature and photoperiod), as such variation could have confounded the estimates of repeatability (Killen et al. 2016).

Angling trials.—After the second behavioral trial, Muskellunge were haphazardly stocked into one of two 0.04-ha ponds (2 m deep × 24 m long × 15 m wide) on October 2, 2021 ($n = 34$ fish/pond), along with approximately 500 Fathead Minnow for forage (Keiling and Suski 2019). Prior to stocking, both ponds were drained, vegetation was manually removed, and pond beds were permitted to air dry for 6 d. Following this 6-d period, ponds were refilled with municipal water and given a 10-d period to dechlorinate (chlorine levels in the ponds fell to under 1 mg/L prior to stocking). After stocking, Muskellunge were given 1 week to acclimate prior to commencement of angling trials. The fish stocked into the ponds did not differ in weight, length, or any of the principal component (PC) scores for behavior described below (t -tests: $t < -1$, $df > 5$, $P > 0.10$).

Angling in both ponds occurred from October 8 to November 11, 2021, with approximately 0.5 h of effort applied to each pond during each angling session. In an attempt to maximize captures and prevent habituation to specific lures (Wilson et al. 2015; Arlinghaus et al. 2017; Louison et al. 2018a), a variety of artificial lures and angling strategies commonly employed by Muskellunge anglers were used at varying times throughout the morning (0700–0900 hours) and afternoon (1500–2000 hours), with a total of 42 person-hours applied by three different anglers. In total, eight different lures were utilized during the experiment; up to two lures were utilized by one

angler within each angling session, with the different lures being deployed haphazardly during a trial. Anglers carried several fishing rods outfitted with different lures so that switches between lures could occur seamlessly throughout a trial, with minimal interruption of fishing effort. After a total of eighty-four 30-min sessions spread across 35 d of angling, the trials concluded and both ponds were drained on November 12, 2021. All 68 Muskellunge that were stocked into the ponds were recovered. Fish that were captured by angling were air exposed for less than 30 s while unhooked and were identified via PIT tag, and all captured individuals were transferred to tanks in the same outdoor holding facility as used before. A group of uncaptured Muskellunge, equal in number to the captured group, was haphazardly selected from the uncaptured population, and those fish were held in outdoor tanks in a manner identical to the holding of captured fish. All Muskellunge were held for 3 d to recover from collection in the ponds before metabolic assessments. Fish in the uncaptured and captured groups did not differ in either TL or weight (t -tests: $t < -1$, $df > 5$, $P > 0.10$).

Metabolic assessments.—Metabolic parameters consisted of standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (AS; Chabot et al. 2016) while accounting for background respiration. To quantify the MMR, Muskellunge were exercised to exhaustion by tail grabbing in a small circular tank, a process that typically required 5 min (Suski et al. 2007). Once they were exhausted and unresponsive to additional tail pinches, Muskellunge were loaded into one of four 7,697-mL, acrylic static respirometry chambers (Loligo Systems, Viborg, Denmark) submerged in a temperature-controlled tank held at 11°C (a temperature matching that of the outdoor holding tanks), where they remained overnight. The measurement cycle during overnight holding was as follows: a 600-s flush period, followed by a 120-s wait and then a 1,200-s measurement period. Dissolved oxygen was measured utilizing a fiber-optic probe every 5 s throughout the measurement period, and the SMR was calculated based on the mean of the five lowest metabolic rate values ($\text{mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$) throughout the overnight measuring period (Nelson and Chabot 2011; Chabot et al. 2016). The MMR was defined as the single highest oxygen consumption value after exercise (Norin and Clark 2016; Louison et al. 2018b), and the AS was defined as the difference between the MMR and SMR (Redpath et al. 2010). Background respiration was quantified by running empty chambers before and after trials with fish and assuming a linear change in oxygen consumption (Rodgers et al. 2016).

Analyses.—Videos from behavioral trials were assessed using the motion-tracking software EthoVision XT version 16.1 (Noldus, Leesburg, Virginia; Noldus et al. 2001; Delcourt et al. 2013), with separate assessments run for each

phase (pre-lure, lure, and mirror) of the behavioral assay. More specifically, during the 10-min pre-lure phase of the behavioral assessments, the software was used to calculate the duration of time for which the fish was in the exploration zone, swimming velocity (total distance traveled/duration of phase), the duration of time spent moving, the duration of time for which the fish was immobile, and the total distance swam. Videos were also manually scored to quantify the time taken for each fish to emerge from the refuge and the number of times the fish emerged from the refuge (emergence frequency) if they returned to the refuge during the trial. During the 10-min lure phase, these identical behavioral metrics were quantified in addition to the duration of time spent motionless after the introduction of the fishing lure (i.e., freeze time) and the number of times the fish inspected the fishing lure (lure inspections). No fish visually inspected or attacked the lure (i.e., fish stopped moving and deliberately oriented toward the lure for more than 1 s; Réale et al. 2007; Keiling and Suski 2019). Finally, during the 10-min mirror phase of the behavioral assay, the behavioral software was again used to quantify all of the behaviors described above in addition to the total number of mirror “displays” performed by each fish. In this study, a display was deemed to have occurred when a fish approached within one body length of the mirror and displayed its fins while exposing its full side to the mirror (Swain and Holtby 1989; Gonçalves-de-Freitas and Mariguela 2006; Way et al. 2015).

Statistical analyses were performed using R version 4.1.1 (R Core Team, Vienna, Austria) and the level of significance (α) was set at 0.05. To determine repeatability of behaviors, the package rptR was utilized (Stoffel et al. 2017). Behaviors were designated as repeatable when the 95% confidence interval of the replicate behavioral scores did not overlap zero (Wolak et al. 2012; Liljequist et al. 2019). After assessing repeatability between trials, 7 of the 23 behavioral variables measured were deemed repeatable (Grossman et al. 1991; Tables 1 and 2). Scores from the two trials were then averaged to produce a single value per repeatable behavior for each individual. A single value per individual was necessary, as the number of replicate trials conducted (2), commonly used in behavioral studies, was not sufficient to utilize a mixed-model approach based on the number of study fish used (68; Martin et al. 2011; Dingemanse and Dochtermann 2013; Tkaczynski et al. 2019; Dingemanse and Wright 2020). Principal components analysis (PCA) was then utilized to distill the collinearity that was present within the repeatable behaviors and to better identify each individual's behavior type (Budaev 2010), using behavioral scores to generate PCs. Suitability of the data for use in PCA was confirmed using a Kaiser–Meyer–Olkin test and Bartlett's test for sphericity (Budaev 2010) with the psych package in R (Revelle and Revelle 2015). Principal components with eigenvalues

TABLE 1. Descriptive statistics for all repeatable behaviors measured in Muskellunge ($n = 68$) during this study (see Table 2 for repeatability metrics).

Variable	Mean	SD	Median
Weight (g)	147.8	24.8	148.0
Frequency of entry to exploration zone (count)	2.1	2.0	1.8
Percentage of time spent at mirror	48.5	32.3	49.0
Distance moved during lure phase (cm)	461.3	447.0	429.0
Mobile time during pre-lure phase (s)	19.7	36.0	6.0
Time in exploration zone during pre-lure phase (s)	294.4	177.3	300.0
Time to first emergence from refuge (s)	262.6	192.7	279.3
Mobile time during lure phase (s)	34.0	61.3	14.9

greater than 1 (of which there were two) were varimax rotated based on maximum likelihood (Grossman et al. 1991), and factors with a loading of at least |0.5| were deemed primary drivers for their PC (Budaev 2010). Rotated loadings were then associated to individual fish.

Values for MMR, SMR, and AS were generated by utilizing the FishResp package (Morozov et al. 2019), accounting for background respiration. For metabolic rate data, the minimum coefficient of determination (r^2) value required for inclusion in the study was 0.95 (Svendsen et al. 2016).

To quantify the impacts of behavior on the likelihood of capture, we ran two separate yet complementary series of analyses, all of which included fish weight as a factor in addition to behavioral PCs because weight has been shown to be an important indicator of capture in prior

studies (Burton et al. 2011; Keiling and Suski 2019; Tsu-boi et al. 2021) and also due to its influence on metabolic rate. Note that weight and TL were correlated (Spearman's rank correlation: $\rho = 0.90$, $P < 0.01$). The first analysis used an information theoretic approach (Akaike's information criterion [AIC]) to identify the variable(s) with the strongest influence on capture. An AIC approach was chosen because it is better suited for work with behavioral variables than hypothesis testing (Wagenmakers and Farrell 2004; Burnham et al. 2011), and it also allowed a number of parameters, along with their interactions, to compete and identify strong predictors, which would be challenging within a hypothesis testing framework. Generalized linear models with a log-link function were generated for the full subset of fish ($n = 68$), with captured/not captured as the response variable, and the independent variables in the models included weight, PC1 score, and PC2 score in additive and interactive combinations (Zuur et al. 2010; Richards 2015). Model strengths were then compared using AIC adjusted for small sample sizes (AIC_c). Top models were selected based on AIC_c difference (ΔAIC_c) values of 2 or less (Wagenmakers and Farrell 2004; Arnold 2010). Pond was not included as a random effect in these models, as random effects cannot be used when there are two or fewer levels in a factor (Bolker et al. 2009; Silk et al. 2020). The performance of all models was assessed via visual examination of Pearson residuals (i.e., quantile–quantile plots to define normality, along with residuals by predicted plots to define homogeneity of variances) using the car package (Menard 2002; Zhang 2016; Fox and Weisberg 2018). Top models were visualized to highlight trends in the data and to define relationships with capture.

The second analysis that was run quantified the impact of metabolic parameters on capture and used the subset of fish for which metabolic parameters (SMR, MMR, and AS) were measured. Because each metabolic parameter

TABLE 2. Results of assessments to define the repeatability of behaviors during laboratory behavioral assays with Muskellunge, conducted across three phases (pre-lure, lure, and mirror). “Pre-lure” refers to the first 10-min segment (0–10 min) of the trial, when animals were allowed to emerge from their refuge; “Lure” refers to the second 10-min segment (10–20 min), wherein a fishing lure was dropped within the tank; and “Mirror” refers to the third 10-min segment (20–30 min), when Muskellunge were allowed to interact with a mirror. In total, 68 Muskellunge were analyzed. Confidence intervals that did not overlap zero were deemed repeatable and were included in subsequent analyses. “Agreement R^2 ” refers to the repeatability level after analysis, and P refers to the associated P -value of the respective metric.

Behavioral session	Behavioral metric	Behavioral axis	Agreement R^2	SE	95% CI	P
Pre-lure	Frequency leaving refuge (count)	Boldness	0.388	0.135	0.081, 0.606	0.003
Pre-lure	Total time in open arena (s)	Exploratory	0.249	0.116	0.013, 0.477	0.024
Pre-lure	Refuge emergence time (s)	Exploratory	0.253	0.111	0.019, 0.481	0.022
Pre-lure	Time moving (s)	Activity	0.348	0.111	0.130, 0.555	<0.001
Lure	Distance moved (cm)	Activity	0.390	0.101	0.198, 0.581	0.012
Lure	Time mobile (s)	Activity	0.437	0.103	0.225, 0.630	<0.001
Mirror	Percentage of time at mirror	Aggression	0.0420	0.000	0.042, 0.042	0.332

was considered a separate biological and statistical predictor of capture and because the sample size was below that recommended for AIC analyses (Jenkins and Quintana-Ascencio 2020), these variables were compared across captured and uncaptured fish by using *t*-tests, and α was Bonferroni corrected to account for multiple comparisons (Killen et al. 2017; Louison et al. 2017; Blasco et al. 2020).

RESULTS

In total, seven behaviors were identified as repeatable (Tables 1 and 2). Utilizing these repeatable behaviors, two PCs were constructed with eigenvalues greater than 1 (Table 3; Figure 1). Principal component 1 explained 44% of the variance in the data and contained boldness- and activity-related behaviors across both the pre-lure and lure sessions. Fish that received high PC1 scores spent a greater duration of time moving in the arena during the pre-lure and lure phases, moved a greater distance after the lure was introduced, and made more emergences from the refuge (Table 3). Principal component 2 explained 36% of the total variance and consisted of exploration- and aggression-related variables (Table 3). Fish that had high PC2 scores took a short amount of time to emerge from the refuge, spent a greater duration of time in the open at the outset of the trial, and spent a longer duration of time at the mirror.

TABLE 3. Factor loadings and variance explained for principal components analysis on behaviors of 68 Muskellunge (PC1, PC2 = principal components 1 and 2). Metrics include the repeatable behaviors that were measured across trials from Table 1, with the respective units in parentheses. The behavioral axis in which the behavior lies is also defined. Factors that loaded negatively (i.e., refuge emergence time) are preceded with a hyphen (-). Values in bold represent the selected metrics within each PC.

Metric	Behavioral axis	PC1	PC2
Frequency leaving refuge (count)	Boldness	0.665	0.427
Total time in open arena before lure (s)	Exploration	0.109	0.953
Refuge emergence time (s)	Exploration	-0.220	-0.950
Time moving pre-lure (s)	Activity	0.875	0.223
Distance moved during lure (cm)	Activity	0.908	0.201
Percentage of time at mirror	Aggression	0.337	0.657
Time mobile during lure	Activity	0.946	0.147
Variance explained		0.443	0.362
Cumulative variance		0.443	0.805

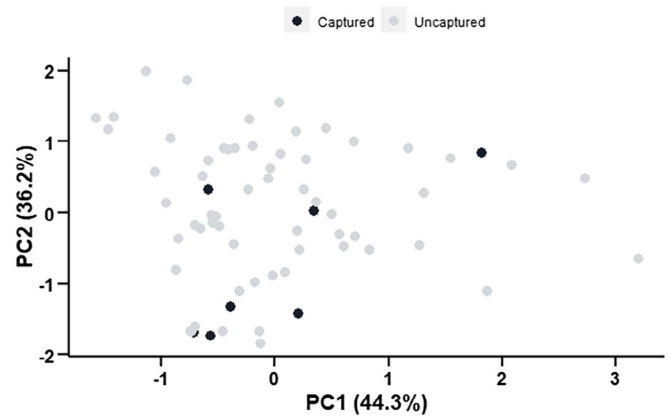


FIGURE 1. Principal components analysis plot, representing the principal component 1 (PC1) scores (boldness and activity) and principal component 2 (PC2) scores (exploration and aggression) among captured (black circles) and uncaptured (gray circles) Muskellunge. Seven of the 68 individuals were captured.

Overall, 42 angler-hours were applied to the two ponds in 30-min increments across 35 d of angling. Capture tallies were highest on the first day, when four fish were captured, and then declined in the following days. In total, seven Muskellunge were captured across all angling sessions, resulting in a CPUE of 0.167 Muskellunge/h of angling. There were no recaptures over the 35 d of angling.

The AIC_c analyses relating behavioral scores to capture (conducted on the full population of Muskellunge that received behavioral testing) found four models with ΔAIC_c values of 2 or less, which were considered the top models. All four models contained PC2 and weight, including additive and interactive models with these variables, highlighting their importance for predicting capture (Table 4). Principal component 1 was not included in any of the models with ΔAIC_c values less than 2 (Table 4), and the fully parameterized model and null model both had ΔAIC_c values greater than 2. When the influence of weight and PC2 was visualized, results showed that captured fish had a lower PC2 score relative to uncaptured fish (Figure 2A) and that captured fish were heavier than uncaptured fish (Figure 2B). Visualizing the interaction between weight and PC2 showed that fish more likely to be captured were heavier and had lower PC2 scores (Figure 2C). For the subset of fish that received metabolic testing, *t*-tests did not identify any significant differences between the captured and uncaptured groups (Table 5).

DISCUSSION

Muskellunge that were less aggressive and less exploratory during behavioral trials were more likely to be captured in the pond angling experiment. More specifically,

TABLE 4. Selection of generalized linear models relating the capture of Muskellunge to different behavioral parameters as well as fish weight. Fish in the population were angled from earthen-bottom ponds by utilizing traditional hook-and-line angling gear. Principal component 1 (PC1) is associated with exploration and activity, while principal component 2 (PC2) indicates aggression and boldness metrics (see Table 3 for specific details on PCs). Weight was measured to the nearest gram. The symbol K indicates the number of parameters within the model, $\text{Log}(L)$ is the log likelihood to assess model fit, AIC_c is Akaike's information criterion adjusted for small sample sizes, and ΔAIC_c indicates the difference in AIC_c of each respective model relative to the top model.

Model	K	$\text{Log}(L)$	AIC_c	ΔAIC_c
PC2 + Weight	4	-18.97	44.32	0.00
PC2 \times Weight	4	-18.499	45.6	1.28
Weight	3	-20.9	46.0	1.68
PC2	3	-20.93	46.05	1.73
PC1 + PC2 + Weight	5	-18.9	46.44	2.12
Null model	2	-22.54	47.14	2.82
PC1 + Weight	4	-20.88	48.13	3.81
PC1 + PC2	4	-20.93	48.24	3.92
PC1	3	-22.53	49.25	4.93
PC1 \times PC2	4	-20.32	49.3	5.02
PC1 \times Weight	4	-20.855	50.3	6.02
Full model	9	-17.798	51.5	7.18

Muskellunge that were captured showed low PC2 scores, which represented low exploration during the initial (pre-lure) portion of the trial, a short amount of time spent outside of the refuge, and a long time to emerge from the refuge, if they actually emerged at all. In addition, Muskellunge that were more likely to be captured also spent a lower proportion of time near the mirror during the mirror test. Animal behavior can be divided into five distinct axes (aggression, sociability, activity, exploration, and boldness; Réale et al. 2007) that are consistent and repeatable across individuals and have been linked to fitness-related outcomes (Dingemanse et al. 2007; Smith and Blumstein 2008). Past work has found that behaviors such as time spent in an open arena as well as the duration of time to first emergence from a shelter before the introduction of a novel object (i.e., the lure) are a part of the exploration axis (Réale et al. 2007; Keiling et al. 2020). In addition, the time spent near a mirror (i.e., within one body length) has been used to define aggression-related behaviors (Gonçalves-de-Freitas and Mariguela 2006; Réale et al. 2007; Way et al. 2015). Past work has shown that behaviors belonging to the exploration and aggression axes predict capture in some fish, but the results have not been consistent across the species examined. For example, Largemouth Bass that were more aggressive during the brood-guarding stage were more likely to be captured compared to less-aggressive individuals (Suski and Philipp 2004), whereas work with Bluegill

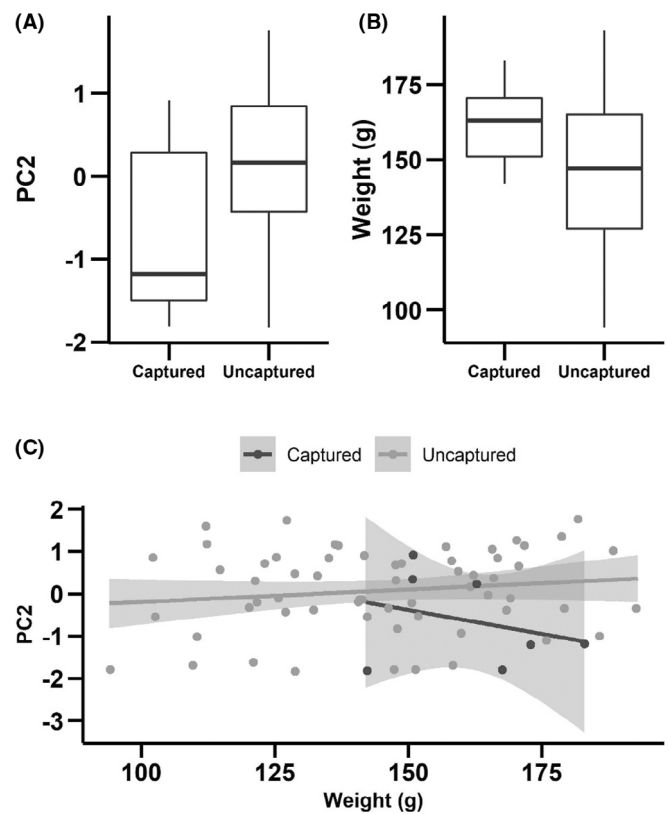


FIGURE 2. Relationship between principal component 2 (PC2) and weight for captured and uncaptured Muskellunge based on the top models shown in Table 4: (A) variation in PC2 between captured and uncaptured fish (see Table 3 for additional details on PCs); (B) weight of captured and uncaptured fish; and (C) interaction between weight and PC2 for captured and uncaptured fish. In panels (A) and (B), the horizontal line within the box represents the median. The ends of each box represent the upper and lower quartiles. The whiskers of each box represent the upper and lower quartile \pm the interquartile range (IQR). In panel (C), gray shadings represent the 50% confidence interval.

TABLE 5. Summary statistics and results of t -tests comparing weight (g), maximum metabolic rate (MMR), standard metabolic rate (SMR), and aerobic scope (AS) across Muskellunge captured by anglers ($n = 7$) or a randomly selected subset of uncaptured Muskellunge ($n = 7$). Metabolic parameters (MMR, SMR, and AS) are all measured in the same units ($\text{mg O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}$). Owing to Bonferroni adjustments to α , significance was assessed at $P = 0.02$.

Parameter	Mean	SD	Median	df	t	P
Weight	162.7	14.6	162.5	12	-0.28	0.78
MMR	114.7	31.4	121.7	12	-0.31	0.77
SMR	75.6	16.3	78.3	12	0.02	0.98
AS	39.1	24.3	46.0	12	-0.4	0.69

Lepomis macrochirus found aggression to be negatively correlated with the likelihood of capture (Louison et al. 2018a, 2018b). For exploration, work with Common Carp

showed that the more exploratory individuals were disproportionately captured relative to more sedentary fish (Klefoth et al. 2017). Additionally, Härkönen et al. (2014) found that more exploratory Brown Trout were five times more likely to be captured in angling scenarios than less-exploratory fish. Muskellunge are selective sit-and-wait predators (Wahl and Stein 1988; Kapuscinski et al. 2012) that remain motionless in the water and use rapid C- or S-start burst swimming to strike prey that approach within an appropriate distance (Webb and Skadsen 1980; New et al. 2001). This ambush foraging style would suggest that Muskellunge that are likely to successfully capture prey are also more likely to remain motionless until prey come within striking distance, potentially explaining why individuals with low PC2 scores (related to low aggression and exploration) were disproportionately captured. Together, results from the current study demonstrate that behavioral factors were important for influencing capture in Muskellunge, with individuals that showed a low tendency to exhibit exploratory or aggressive behaviors being captured more frequently than individuals that were more exploratory and aggressive.

In addition to aggression- and exploration-related metrics, the weight of Muskellunge was also an important predictor of capture. More specifically, results indicated not only that larger (heavier) Muskellunge were more likely to be captured than smaller conspecifics, but also that there was an interaction of size and behavior such that the likelihood of capture was higher for heavier fish with lower PC2 scores. A number of previous studies have demonstrated a positive correlation between fish size and the probability of capture (Biro and Post 2008; Vainikka et al. 2012; Klefoth et al. 2017; Keiling et al. 2020). For example, larger Common Carp (TL [mean \pm SD] = 201.6 \pm 10.0 mm) have been shown to be more active, bold, and exploratory compared to smaller fish (198.0 \pm 8.4 mm)—behaviors that are associated with foraging success and capture in angling scenarios (Härkönen et al. 2014; Klefoth et al. 2017). Relationships between size, behavior, and capture have also been demonstrated in Largemouth Bass, wherein larger males were shown to be more aggressive toward lures when nest guarding and were captured more often than smaller conspecifics (Suski and Philipp 2004). Larger fish have been shown to be dominant over smaller fish, resulting in a competitive advantage for larger fish relative to smaller conspecifics for factors such as habitat selection and resource acquisition (Krause 1994; Yamamoto et al. 1998). Furthermore, larger fish have higher consumptive requirements than smaller fish, leading to foraging behaviors that increase the likelihood of capture (Hessenauer et al. 2015; Tsuboi et al. 2016; Lennox et al. 2017; Keiling et al. 2020). All Muskellunge in the present study came from a single hatchery cohort and were therefore of identical age. The weight of captured fish in the current study ranged from

142 to 183 g, while the full population of fish ranged from 94 to 183 g, representing a relatively narrow size distribution among captured and uncaptured individuals. Despite this, Muskellunge that were captured were larger, less exploratory, and less aggressive, behaviors that likely maximize foraging success for the sit-and-wait aquatic predator (Wahl and Stein 1988; Kapuscinski et al. 2012). Although we saw no difference in either resting metabolic rate or AS across captured and uncaptured individuals, it is also possible that larger fish had higher growth rates or higher feed efficiency (weight gain per unit consumption; Forster 2011), allowing them to reach larger sizes than others in their cohort. While the sizes of fish captured in the present study are smaller than what an angler may target, the behaviors of animals are repeatable and consistent over time (Réale et al. 2007; Bell et al. 2009), indicating that larger-sized fish may exhibit similar behavioral predictors of capture. However, there persists a need for future work to detail the behavior of targeted fish over longer time periods (i.e., months or years). Large size was a predictor of capture in Muskellunge and, in particular, larger Muskellunge that were less exploratory and less aggressive toward conspecifics showed an increased likelihood of capture.

For Muskellunge in the current study, bold behaviors, behaviors related to activity, and metabolic parameters did not influence capture. Boldness and activity are distinct behavioral axes (Réale et al. 2007), and both have been shown to correlate positively with angling vulnerability in Common Carp, which is likely related to foraging style, as Common Carp are mobile benthivores (Klefoth et al. 2017) in contrast to the sit-and-wait, ambush foraging style of Muskellunge (New et al. 2001; Crane et al. 2015). Past work has also found that fish with higher metabolic rates were captured more often than individuals with lower metabolic rates (Biro and Stamps 2010; Redpath et al. 2010). Metabolic rate—specifically AS—measures an organism's use of energy and capacity for aerobic processes (Fry 1971; Killen et al. 2012). Individuals that have high AS typically require more food (Chabot et al. 2016) than lower-AS individuals in an effort to attain the required resources to meet energy demands, which may subsequently increase vulnerability to angling as animals seek food (Biro and Post 2008; Biro and Stamps 2008; Réale et al. 2010; Redpath et al. 2010; Metcalfe et al. 2016). Prior work has also demonstrated that hunger can lead to increases in exploration and activity that may elevate the probability of interacting with a lure (Beukema 1968; Keiling et al. 2020), potentially linking an individual's metabolic rate to the likelihood of capture. However, the impact of metabolic rate on angling vulnerability is not always clear and may be species specific, with some studies showing that metabolic rate did not predict capture (Uusi-Heikkilä et al. 2015; Ballew et al. 2017;

Louison et al. 2017, 2018b). Regardless of the mechanisms, metabolic rate, activity, and bold behaviors were not key drivers that predicted capture in Muskellunge.

The capture rate of fish in experimental settings as well as in natural populations will decline over time with consistent angling pressure. The observed decline in capture rate in the current study was therefore unavoidable and expected (Beukema 1970; Askey et al. 2006; Koeck et al. 2019). The CPUE in the current study was higher than those in comparable studies with wild populations (see the Supplement available in the online version of this article), although the density of fish in the present study was likely higher than that of wild populations (Shaw et al. 2021). Reasons for the trends in capture during the current study are not known, but we propose three possible explanations. First, prior work has indicated that food deprivation can lead to more lure inspections (Largemouth Bass: Keiling and Suski 2019; Keiling et al. 2020) and increased activity (Qingbo *Spinibarbus sinensis*: Wang et al. 2019) relative to fed conspecifics. The ponds in the present study were stocked with minnows to maintain health during holding, and these well-fed Muskellunge may not have been engaging in lure inspections, which may have contributed to low capture rates. Second, though not directly quantified, other fish species have demonstrated lure avoidance learning, either through direct experience or through the “social learning” experience of observing another individual being captured (Askey et al. 2006; Louison et al. 2018a; Wegener et al. 2018; Lovén Wallerius et al. 2020). Therefore, the low overall capture rate may have occurred due to learning as Muskellunge developed a negative association with lures or the presence of anglers at the ponds. Finally, among the appealing factors that make Muskellunge a popular target for anglers are their wariness and difficulty to catch, and there may be other factors not assessed here that may drive capture. For example, Shaw et al. (2021) analyzed a 12-year data set of Muskellunge capture on Escanaba Lake, Wisconsin, and found that factors such as the use of live bait, lunar phase, and barometric pressure all influenced the capture of Muskellunge, but these factors were not accounted for in the current study design. Although the exact mechanism for low overall capture is not clear, the present study was successful in capturing fish relative to other work conducted with wild Muskellunge. Additional mechanisms that may define why Muskellunge show lower susceptibility to capture relative to other game fish species should be pursued in the future.

The capture of fish through hook-and-line angling can lead to incidental mortality that can directly influence fish communities by reducing population size (Cooke and Suski 2005). In addition, the removal of fish with certain traits, such as body size (growth rate), boldness, or metabolic parameters, can have indirect impacts on the composition

of populations that can lead to declines in vulnerability or possible long-term reductions in reproductive output (Réale et al. 2007; Arlinghaus et al. 2017). Gaining insight into traits that predispose fish to capture is valuable for sustaining angler satisfaction (Birdsong et al. 2021) and can help with the long-term management of fish populations. In the present study, Muskellunge that were larger, less exploratory, and less aggressive were preferentially captured, while metabolism, boldness, and activity did not influence capture. This finding provides critical information for managers looking to both maintain angler catch rates for Muskellunge and ensure longer-term sustainable use of fisheries resources. More specifically, the results emphasize that these valuable and vulnerable phenotypes should be protected and allowed to reproduce. Although release rates for Muskellunge after capture are presumably high (Fayram 2003), trophy harvest can occur, incidental hooking mortality is possible, and angling-induced postrelease mortality can also occur (Bartholomew and Bohnsack 2005; Cooke and Suski 2005), particularly at high water temperatures (Booth 2022; Jenkins 2022). Thus, sustained angling for Muskellunge could lead to a reduction in vulnerable phenotypes from a population and a subsequent evolutionary response. Selection for less-vulnerable individuals could also impact population-level parameters, such as the timing of maturation, growth rate, and immune function, through pace-of-life relationships, further eroding capture rates (Réale et al. 2007, 2010; Arlinghaus et al. 2017). One specific management activity that could be implemented to conserve valuable phenotypes is the promotion of best practices for fishing, including avoiding fishing in periods of high air and water temperatures to reduce thermal stress (Booth 2022), minimizing air exposure to reduce physiological disturbances (Wilkie et al. 1996), and minimizing fight times with appropriately sized fishing gear to reduce disturbances, ideally minimizing angling-induced mortality (Landsman et al. 2011; Brownscombe et al. 2017). Managers may also consider the development of protected no-fishing areas, thereby preventing incidental mortality and harvest and resulting in the protection of vulnerable phenotypes. This, in turn, may maintain catch rates over time. Protected no-fishing areas have been promoted as a method to protect valuable phenotypes in Largemouth Bass fisheries (Cooke et al. 2017; Twardek et al. 2017) and may also be applicable to other fisheries. The results from this study collectively provide valuable insights into the mechanisms responsible for capture in Muskellunge and highlight a possible target for management actions that can help to sustain populations and support catch rates over time.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.