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Food availability influences angling vulnerability in muskellunge

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Abstract

Reduced food availability increases the capture of several fish species, although the mechanisms responsible for how food resources result in increased capture are undefined. Our objective was to quantify the mechanism by which food availability might influence the angling vulnerability of muskellunge (*Esox masquinongy*). We assessed capture rates in the field under different food levels, quantified the behaviors of muskellunge that were either fed or food deprived, and determined if appetite-related hormones leptin and ghrelin affected fish behavior. Catch rates of fasted muskellunge were more than twice as high as those of fed muskellunge. However, food deprivation and hormonal treatments did not influence laboratory behavior, which suggested that catch rates of food-deprived muskellunge increased because fish were more receptive to lures. Furthermore, an ecosystem approach should be used to consider forage as a component of management goals.

KEYWORDS
angling vulnerability, behavior, conservation, ecosystem stressor, management

1 | INTRODUCTION

For a fish to strike an angling lure, three conditions must align. First, the angler and the fish must overlap spatially such that angling gear is presented in a way that it is encountered or perceived by a fish. This overlap of anglers and fish can be considered from both a small-scale perspective (i.e., nearshore vs. offshore environments within an individual waterbody; Matthias et al., 2014) or from a landscape-scale perspective, with anglers considered mobile predators moving from waterbody to waterbody based on capture success (Post et al., 2008). Second, the internal state of the fish must make it vulnerable or receptive to angling gears, also known as an angling-vulnerable state (Lennox et al., 2017). In many cases, the motivation for a fish to strike a lure is driven by feeding (Baur et al., 1976; Raat, 1991; Ware, 1972), which can be influenced by internal factors such as hormones that regulate metabolism or external factors such as food or temperature (Einen et al., 1998; Fry, 1971). Lure striking

can also result from factors other than food or feeding, including territory or brood defense (Suski & Philipp, 2004) or repeatable behavioral characteristics that motivate lure striking in fish, with behaviors such as aggression, activity, boldness, or hormone responsiveness influencing capture (Bieber et al., 2023; Klefoth et al., 2017; Louison et al., 2017, 2018). Last, a lure must be presented in a way that induces striking behavior (i.e., fish must be receptive to the lure), which can be influenced by factors such as size of the lure relative to size of the fish, novelty, habituation, lure behavior, or lure type (Gaeta et al., 2018; Lennox et al., 2017; Nieman et al., 2020; Stålhammar et al., 2014).

Prey availability can alter the vulnerability of fish to angling capture. More specifically, fish are captured more often when prey availability is low (Lennox et al., 2017; Mogensen et al., 2014; Raat, 1991), thereby indicating that low prey availability causes fish to be more vulnerable to angling gear. The mechanism responsible for increasing vulnerability to angling has not been defined and could be the

result of several different factors. For example, low food resources can lead to behavioral changes, such as increased activity that leads to more encounters with angling gear and increased capture. Alternatively, low food resources can alter the internal state of a fish, which could lead to increased capture by anglers due to upregulation of appetite-related hormones and an increase in willingness to strike a lure. Low food resources may also influence susceptibility of individual fish to angling lures by heightening reception of lures to broader spectrums of colors, shapes, or sizes. By defining mechanisms responsible for increasing angling vulnerability, managers can understand how target species in waterbodies behave in response to different stimuli and situations that make fish more susceptible to harvest or hooking mortality. In turn, this can result in more effective management of recreational fisheries that may be experiencing declining capture rates or population sizes. For example, managers may be able to understand and revise stocking programs to enhance capture and angler satisfaction within a system. In addition, managers can adjust pretty stocking programs in a way that could lead to the development of trophy fishery (e.g., increased growth rates) or higher catch rates with smaller fish, which may help achieve management objectives for different systems.

One of the most iconic and popular freshwater fish in North America is the muskellunge (*Esox masquinongy*; Fayram, 2003; Glade, 2021). This top predator occupies lakes and streams in North America and is a target for anglers year-round (Fayram, 2003). The life span of muskellunge can exceed 30 years (Casselman & Crossman, 1986), and, like many fish, muskellunge may experience fluctuations in food availability and multiple captures by anglers over their lifetime. Furthermore, muskellunge are a species commonly stocked in North America, with 46% of all waters containing muskellunge as a result of introduction and 36% of those supported through stocking efforts (Kerr, 2011). As a result, the muskellunge is an ideal model for asking questions related to how behaviors and angling vulnerability influence the transition to an angling vulnerable state in the context of high and low food availability, which can inform management activities such as prey stocking that may influence capture by anglers, as well as the growth and overall size of the muskellunge within the system.

Our objectives were to determine if food deprivation affected the capture of muskellunge by anglers and to define a possible mechanism by which food might influence the response to angling in this species. To accomplish this goal, we conducted three complementary experiments using hatchery-reared, angling-naïve muskellunge. First, we experimentally angled muskellunge from ponds that contained either forage or no forage to compare the proportion of captures among treatments. Second, we fed or withheld food from a group of muskellunge and quantified changes in behaviors (boldness, aggression, and exploration). Finally, we conducted a preliminary experiment to explore if two appetite-related hormones affected these behaviors. Together, these experiments provided important information on how food availability influenced the behavior of muskellunge and possible mechanisms to explain links between food availability and capture. This information could provide critical

information to managers to inform possible strategies to increase or decrease catch rates within waterbodies (e.g., supplemental stocking of prey) and facilitate conservation of this species.

2 | METHODS

2.1 | Fish

On September 30, 2022, 196 age–0 muskellunge were transported from the Illinois Department of Natural Resources (IDNR) Jake Wolf Memorial Fish Hatchery in Topeka, IL [mean total weight = 146.9 g ± 2.4 g standard error (SE); mean total length = 310.2 mm ± 2.4 mm SE] to the Aquatic Research Facility at the University of Illinois, Urbana, IL. These age–0 muskellunge are stocked throughout Illinois, are comfortable indoors, are available in sufficient numbers for this study, and are consistent in behavioral characteristics across ontogeny (Bell et al., 2009), which made them ideal for this work. At the research facility, fish were distributed into 10 outdoor, 1135–L holding tanks connected via flow-through to an adjacent earthen-bottom pond. On October 2, 2022, after a 48-h period, fish were implanted with a passive integrated transponder (PIT) tag (Biomark Inc.) within the peritoneal cavity without anesthetic for individual identification (Wagner et al., 2007). Tagged fish were returned to holding tanks to recover for 48 h prior to the start of experiments and fed fathead minnows (*Pimephales promelas*) from Keystone Hatchery, Sullivan, IL, USA, ad libitum. Individual muskellunge were assigned to one of three experimental groups: an angling assay group ($n = 140$), a feeding or fasting assay group ($n = 23$), and a hormone manipulation group ($n = 33$).

2.2 | Food availability experiment

Four identical, earthen-bottom ponds (0.04 ha, 2 m deep × 24 m long × 15 m wide) were drained, vegetation was removed by hand, and the ponds were allowed to air dry for 10 days. A 10 m × 2.5 m tarpaulin was placed in the center of each pond and held in place with bricks to act as a vegetation suppressant and to provide a standard angling area. Ponds were filled with municipal water and allowed to dechlorinate for 14 days, after which chlorine levels were 0 ppm (Chlorine test strips ECO203110111, Ecolab).

Two of the four ponds were stocked with 1000 fathead minnows for forage (Keiling & Suski, 2019), and the other two ponds were stocked with no supplemental forage. Of the one hundred and forty tagged muskellunge, thirty-five were stocked into each of the four ponds on October 3, 2022. Stocked muskellunge were allowed to acclimate for over 1 week prior to the commencement of angling trials. Fish stocked into ponds did not differ significantly in mean length (one-way ANOVA, $F_{3,136} = 0.213$, $p = 0.887$) or weight ($F_{3,136} = 0.343$, $p = 0.794$).

During October 12–18, 2022, a single experienced angler fished each pond for four 30-min sessions across 7 days. Acclimation and

angling time resulted in 14-days of food deprivation to minimize the likelihood of food deprivation impacting angling or fish behavior (Gingerich et al., 2010). A variety of gears and techniques commonly used by muskellunge anglers were used, sized appropriately for fish in ponds, including spinner baits, "twister" baits, tube lures, plastic flukes, and minnow lures (colored white, pink, yellow, orange, or navy) fished at a variety of depths, speeds, and angles (Bieber et al., 2023). An effort was made to cast to all areas of ponds with the same combination of lures and angling strategies in all ponds. Captured fish were identified by individual PIT tags, examined for hooking injuries (none were recorded), and immediately returned to the water with the minimum interruption to angling or air exposure (typically <30s). During October 18–19, 2022, after 7 days of angling (14 days following the initial stocking of fish), ponds were drained. Of the 140 muskellunge stocked into ponds, 136 were recovered.

2.3 | Feeding and fasting experiment

In open-field behavioral assays (Réale et al., 2007), twenty-three different muskellunge were used to define how behaviors previously shown to influence angling vulnerability in muskellunge [aggression and exploration (Bieber et al., 2023)] might change as a result of food deprivation. On October 8, 2022, initial behavioral assays that used all twenty-three muskellunge to generate baseline behavior data consisted of a 15-min trial broken into three 5-min segments (Bieber et al., 2023). Behavioral assays were conducted between 0730 and 1800 within one of four identical indoor arenas composed of a 565 L (181 cm long × 65 cm wide) rectangular polyethylene stock tank filled with water to a depth of 15 cm that was isolated on all four sides with blackout curtains to eliminate external stimuli (Bieber et al., 2023). Arenas were divided into a refuge zone and an open zone. The refuge zone contained gravel substrate and was about one-third of the tank area. This zone was covered with a lid and was separated from the remainder of the arena via a divider attached to a pulley. The remaining two-thirds of the stock tank was an open zone, uncovered, with no substrate. On the side of the tank opposite the refuge area, a mirror (15 cm × 60 cm) 0.5 cm from the bottom of the tank was in a position easily visible to fish. The mirror could be fully concealed by a barrier attached to a pulley. Each arena had a video camera (Sony Handycam CX405, Sony Corp.) mounted above the tank on the refuge side.

Each behavioral assay included a pre-lure exploration segment, a lure segment to quantify the response to a novel object (a fishing lure), and a mirror segment to quantify aggression. Fish were allowed to acclimate within the refuge for 10 min before each trial, a duration that was sufficient to become calm, based on preliminary trials (Bieber et al., 2023). After acclimation, video recording began, and the barrier at the end of the refuge was lifted to allow fish to leave the refuge area, quantified as time inside and outside of the refuge (Bieber et al., 2023; Réale et al., 2007). After 5 min of exploration, a hookless fishing lure (soft-plastic white minnow, typically used in muskellunge angling) was dropped into the center of the arena as

a novel object to provide a stimulus to measure boldness (Bieber et al., 2023; Keiling & Suski, 2019; Näslund & Johnsson, 2016; Réale et al., 2007). Five minutes after the presentation of the lure (10 min after the start of the behavioral trial), the cover in front of the mirror was removed to allow fish to see their reflection, a method commonly used to assess aggression (Baran & Streelman, 2020; Bieber et al., 2023; Way et al., 2015). After the mirror segment (15 min after the trial started), recording was stopped, and muskellunge were returned to outdoor holding tanks.

Following this initial assessment, muskellunge were assigned to one of two treatment groups: a "fasted" group (n = 12) and a "fed" group (n = 11), with each group held in separate outdoor holding tanks. Over 5 days, muskellunge in the "fed" group were fed fathead minnows to satiation daily, whereas the "fasted" group received no forage. Fish in these two treatments could not be comingled because fish in the fasted group could not have access to food. On October 13, 2022, a second behavioral assay, identical to the first behavioral assay, was conducted. The only difference in the second assay was that the dropped lure was changed to a deep navy, neon yellow spinner bait to prevent habituation to the lure stimulus (White et al., 2013). Fed and fasted treatment groups did not differ significantly in mean length (ANOVA, $F_{1,21} = 0.010$, $p = 0.920$) or weight (ANOVA, $F_{1,21} = 0.174$, $p = 0.681$).

2.4 | Hormone experiment

To determine if the hormones leptin and ghrelin affected muskellunge behavior, a final series of experiments was conducted. Ghrelin acts as an appetite stimulant in fish, by increasing foraging and swimming activity of Nile tilapia (*Oreochromis niloticus*), rainbow trout (*Oncorhynchus mykiss*), and goldfish (*Carassius auratus*) (Jönsson et al., 2007; Shepherd et al., 2007). Leptin is linked to fat levels and acts as a satiety signal in a variety of taxa by reducing activity and food intake (Volkoff et al., 2003; Zhang and Chua 2011). Therefore, we hypothesized that muskellunge treated with ghrelin (an orexin hormone) would reduce aggression and exploration (Bieber et al., 2023). A group of thirty-three muskellunge were fasted for 48 h, after which 33 (n = 11 per treatment group) were anesthetized with 50 mg/L of buffered MS-222 (Tricaine methane sulfonate) for surgery. When fish were unresponsive, an Alzet 1007D micro-osmotic pump (DURECT Corp.) was implanted into a 1-cm incision in the peritoneal cavity, and the incision was closed with a single suture (3–0 absorbable sutures). Micro-osmotic pumps were filled with 100 μL of 550 ng/μL of leptin (Enzo Life Sciences, catalog # 89143–978, product #201-034-M001) or ghrelin (Novus Biologicals, catalog #H-5946.1000BA, product #4042605.1000) dissolved in teleost saline (10 mL Na_2CO_3/L of 0.6% NaCl) or a pump filled with saline only (Blanco & Soengas, 2021; Murashita et al., 2011; Tinoco et al., 2014; Unniappan & Kieffer, 2008). The specified release rate for each pump was 0.5 μL/h for 7 days, so the release rate (using the manufacturer's specifications) of hormone was 0 (saline) or 1.1 ng/g/h for leptin and ghrelin. The effects of these hormones on

muskellunge have not been studied previously, so doses were based on studies of other species that reduced the growth of juvenile Atlantic salmon (*Salmo salar*) that were smaller than muskellunge in our study (Atlantic salmon mean body mass 96.5 ± 2.1 g) (Murashita et al., 2011). Length (ANOVA, $F_{2,30} = 1.368$, $p = 0.270$) and weight (ANOVA, $F_{2,30} = 1.852$, $p = 0.175$) did not differ significantly between hormone treatment groups.

On October 13, 2022, 24 h after implanting osmotic pumps in muskellunge (Gullapalli et al., 2012), an initial behavioral assay was conducted to evaluate hormone effects, identical to the one described above, using the same behavioral arenas. On October 18, 2022, after 5 days without food, a second behavioral assessment was undertaken (all fish survived this 5-days period). A delay of 5 days between tests is common in hormone studies to quantify behavioral changes in fish (Ceinos et al., 2008; Figueroa et al., 2001). Following the second behavioral assay, 5 days after implanting, three fish with a saline pump, three fish with a leptin pump, and three fish with a ghrelin pump were selected for a 0.5 mL blood draw from the caudal vessel, without anesthetic, to assess hormone levels at the end of the experiment, a duration commonly used in similar studies (Gentle et al., 2013; Gullapalli et al., 2012). Whole blood samples were centrifuged at 1000 g (gravity) for 2 min. Plasma was removed with a pipette and flash frozen in liquid nitrogen before being stored at −80°C. Duplicate samples of leptin and ghrelin were assayed using commercially available kits and manufacturer directions (Leptin kit, Enzo Life Sciences, Catalog #ADI-900-028A, Lot # 02032220, Ghrelin kit, Novus Biologicals, Catalog # NBP2-60645, Lot # 102282203). Kits were previously used to measure leptin and ghrelin in fishes (Audira et al., 2018), and data on the accuracy and precision of the ELISAs is included in Appendix S3.

2.5 | Statistical analysis

To define the role of food availability in the capture of muskellunge, we used two complementary approaches. First, the proportion of angler captures was compared between treatments (fed vs. fasted) using a two-way binomial logistic regression using base R, version 4.2.2 (R Core Team 2022), with the proportion of total captures across angling sessions as the response variable and treatment (fed vs. food-deprived ponds) as the predictor variable. Second, to quantify the change in capture rate over time between treatment groups, a generalized linear model (GLM) with a Poisson distribution for count data was used, with the number of fish captured (a count) as the response variable and angling sessions (sessions 1, 2, 3, or 4), treatment (fed vs. fasted), and the interaction between treatment and session as predictors. Pond was not included as a random effect because random effects cannot be used for factors with 2 or fewer levels (Bolker et al., 2009; Silk et al., 2020), so ponds were pooled across captures.

Motion tracking software (Ethovision XT® Version 16.1, Noldus, VA; Delcourt et al., 2013; Noldus et al., 2001) was used to analyze videos from behavioral trials, standardize analyses, avoid observer bias, and collect metrics that would have been challenging for human observers (Holman et al., 2015). Video analyses were used to generate data on activity metrics that included distance moved, velocity, and rotation. A single observer (J.F.B.) quantified the duration of time fish spent in the open arena, the frequency (count) of the number of times fish exited and returned to the shelter, and the time to emerge from the shelter at the beginning of the assay (Appendix S1 and S2) (Bieber et al., 2023).

Principal component analyses (PCA) using the "psych" package [version 2.2.5 (Revelle & Revelle, 2015)] were used to quantify the collinearity of measured behaviors in assays involving behavioral metrics (feeding or fasting and hormone manipulation; Budaev, 2010). The suitability of the data for PCA was confirmed using a Kaiser-Meyer-Olkin (KMO) test and Bartlett's test for sphericity (Budaev, 2010). Variables were excluded from subsequent analysis if KMO <0.6 (Budaev, 2010; Keiling & Suski, 2019). Behaviors related to activity (e.g., distance moved and swim velocity) did not have KMO values >0.6 and were subsequently excluded from the PCs. Two principal components with eigenvalues greater than one were varimax rotated using maximum likelihood (Grossman et al., 1991), and factors with loadings ≥|0.5| were deemed primary drivers (Budaev, 2010). Rotated loadings were then associated with individuals within each treatment. Two-way linear mixed effects models in the "lme4" package (version 1.1–29, Bates et al., 2015) were used to quantify the effect of each treatment (feeding vs. fasted; leptin vs. ghrelin vs. saline), iteration (initial vs. repeat test), and the interaction of treatment by iteration on fish behavior. In each model, fish identification (based on the PIT tag) was included as a random effect because multiple measurements were collected from each fish over time, so each measurement was not independent and potentially correlated (Laird & Ware, 1982; Lindstrom & Bates, 1990). Marginal and conditional r^2 values were calculated using the MuMIn package (Bartoń, 2022). For all models, length was included as an interaction with treatment, but was removed if nonsignificant, (Harrison et al., 2018). This experimental design did not permit calculation of repeatability metrics for individual fish across iterations due to a sample size less than 15 and only one video assessment per individual per iteration (Niemelä & Dingemanse, 2017; Wolak et al., 2012).

The suitability of models was assessed by examination of Pearson residuals (i.e., quantile-quantile plots to define normality, residuals from predicted plots to define homogeneity of variances) using the "car" package version 3.0–13 (Fox & Weisberg, 2018; Menard, 2002; Zhang, 2016). For all significant models, Tukey tests using the "emmeans" package [version 1.7.4–1 (Lenth et al., 2021)] were run to identify significant pairwise differences across factors. Significance (α) for all tests was ≤0.05, and effects are shown as means ± SE.

3 | RESULTS

Angling caught 20 fish from ponds without minnows and nine fish from ponds with minnows (Figure 1). Two fish were caught twice. The proportion of captures from ponds without forage was

significantly greater than from ponds with minnows (logistic regression, $X_2 = 6.9$, df = 1, $p = 0.004$). The number of captures was highest during the first angling session, with eleven fish caught from ponds without minnows and four fish caught from ponds with minnows (Figure 1; Table 1). The number of captures declined significantly with time, but the rate of decline was similar between
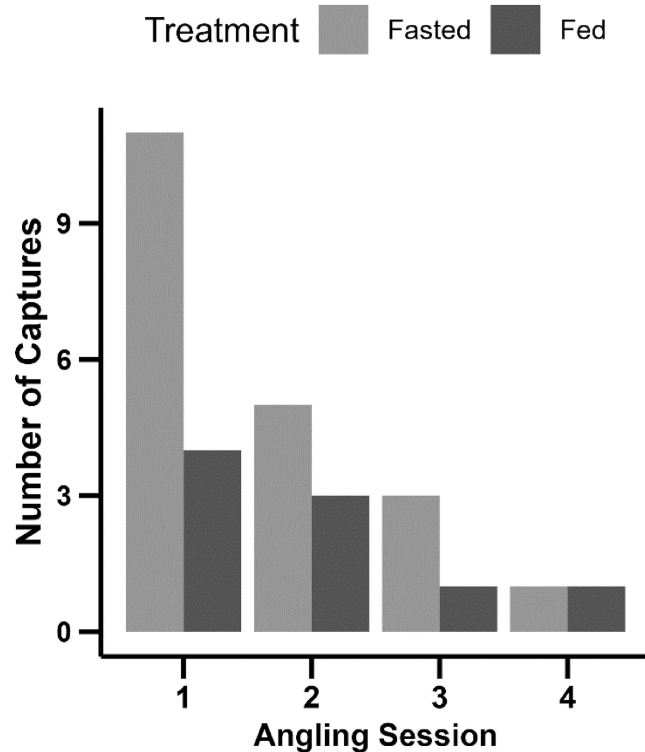
treatments (Table 1; Figure 1). Total length and weight did not differ significantly between captured and uncaptured fish (Total Length: t-test, $t = 0.0054$, df > 105.78, $p > 0.9957$; Weight: t-test, $t = 0.0009$, df > 111.83, $p > 0.9993$).

Two principal components for the feeding and fasting assay included seven behaviors across three axes. Fish in the feeding treatment had 2 PCs that accounted for nearly 78% of the total variance. PC1 consisted of behaviors related to boldness and aggression, and PC2 consisted of behaviors related to exploration (Table 2). Behaviors related to activity (e.g., distance traveled and swimming velocity) did not have KMO values >0.6 and were not included in PCs.

Five days of food deprivation resulted in significant changes in the behavior of muskellunge (Table 3; Figure 1). PC1 increased over time, independent of treatment, and fed muskellunge had higher PC1 scores than food-deprived muskellunge, likely due to a disproportionately high PC1 score for the initial trial of fed fish, despite assigning fish to each category following the initial behavioral trial. Food deprivation did not significantly change behaviors related to boldness and aggression in PC1 or behaviors related to boldness or exploration in PC2 (Table 3; Figure 2b).

For muskellunge treated with ghrelin, leptin, or saline, 2 PCs described 72% of the total variation in behavioral data. PC1 described exploratory behaviors, and PC2 described boldness and aggression behaviors (Table 2). PC1 scores declined significantly between initial and repeat treatments (Table 3; Figure 3a). The interaction between treatment and iteration was also significant for PC2 (Table 3), although no pairwise comparisons were significant (Table 3; Figure 3b). Following hormone treatment with osmotic pumps, the average concentration of leptin was 0.408 ng/mL and that of ghrelin was 0.600 ng/mL (Table 4). Intra-assay variation of ghrelin was 3.12%, and sensitivity was 0.056 ng/mL.

FIGURE 1 Capture of muskellunge across angling sessions: Barchart showing the total number of captures of muskellunge across 4 angling sessions (from October 12 to 18, 2022) in 0.5 ha experimental ponds at the INHS aquatic research facility in Champaign, IL. The ponds contained thirty-five muskellunge each. Two received no forage (fasted) for 7–14 days and two ponds were supplied with approximately 1000 fathead minnows each for forage (fed) over 7–14 days. The light gray bars show the number of muskellunge captured with the fasted treatment per session, and the dark gray represents number of muskellunge captured with the fed treatment. Results of statistical testing showing changes in captures over time are shown in Table 1.

4 | DISCUSSION

Food deprivation did not result in changes in the behavior (boldness, aggression, and exploration) of muskellunge in our study, unlike previous studies (Bell et al., 2009; Sih et al., 2004; Sih & Bell, 2008). The physiology and behavior of individuals interact to modulate the behavior of individual fish in a predictable manner

TABLE 1 Table of statistical results comparing changes in angling capture over time.

Response variable	Factor	LR χ^2	Df	p
Capture number	**Treatment**	**13.477**	**3**	**<0.004**
	Session	**4.279**	**1**	**0.039**
	Treatment × session	0.670	3	0.880

Note: Results of a generalized linear model (GLM) with Poisson error distribution quantifying the change in numbers of muskellunge captured by anglers across treatments and angling sessions. The ponds contained thirty-five muskellunge each. Two ponds received no forage (fasted) for 7–14 days and two ponds were supplied with approximately 1000 fathead minnows each for forage (fed) over 7–14 days. Ponds were fished in 30-min sessions, with 4 sessions total per pond from October 12 to 18, 2022. Capture number of muskellunge is the response variable for the model, and factors (predictors) are angling session, and whether or not ponds contained food (fasted vs. fed). Significant terms are shown in bold.

TABLE 2 Loadings for principal components.

Metric	Feeding and fasting assay		Hormonal assay	
	PC1	PC2	PC1	PC2
Duration of time to emerge refuge (s)	−0.509	**−0.763**	**−0.785**	−0.283
Duration of time in open arena before lure (s)	**0.611**	0.462	**0.563**	0.467
Frequency of entry to open arena before lure (count)	0.149	**0.886**	**0.905**	–
Duration of time in open arena with lure (s)	**0.837**	–	–	**0.842**
Frequency of entry to open arena with lure (count)		**0.849**	**0.815**	0.133
Frequency of entry to open Arena with mirror (count)	**0.839**	0.187	0.250	**0.743**
Duration of time in open arena with mirror (s)	**0.859**	0.169	0.237	**0.811**
Variance explained	0.400	0.339	0.362	0.320
Cumulative variance	0.400	0.739	0.362	0.682

Note: Factor loadings and variance are explained for principal components analysis on behaviors in muskellunge for both feeding and fasting assays and hormonal assays. Twenty-three muskellunge in a laboratory setting underwent two behavioral assays with a duration of 5 days between iterations for feeding and fasting assays. Muskellunge were either fasted or fed to satiation with fathead minnows, and the initial assays conducted on October 8, 2022 and repeat assays were conducted on October 13, 2022. Thirty-three muskellunge were assessed within the hormonal assays, with 11 individuals implanted with leptin, ghrelin, or saline. Individuals were first anesthetized with 50 mg/L of buffered MS-222, and implanted (via a 1 cm incision in the peritoneal cavity) with a micro-osmotic pump (Alzet 1007D micro-osmotic pump from DURECT Corp.) containing either 100 μL of 550 ng/μL of leptin, ghrelin, or 100 μL of a teleost saline solution (10 mL Na_2CO_3/L of 0.6% NaCl). Following a 24-h recovery period, the initial hormone behavioral measurement was conducted on October 13, 2022, and the repeat test was conducted on October 18, 2022. Metrics include behaviors that were measured across trials with the respective trial assay in parentheses. Factors that load negatively are preceded with a hyphen (–). Bold text indicates the measured behaviors loaded into either PC1 or PC2.

TABLE 3 Statistical outputs of LMER models: Model outputs for generalized linear mixed models (GLMER), with Fish ID set as a random factor, quantifying how treatment and iteration impacted behaviors.

Treatment	Response	Factor	χ^2	Df	p	$r^2_{Marginal}$	$r^2_{Conditional}$
Feeding	PC1	**Treatment**	**6.968**	**1**	**0.008**	0.300	0.386
		Iteration	**12.495**	**1**	**0.004**		
		Treatment × iteration	0.527	1	0.468		
	PC2	Treatment	0.617	1	0.432	0.026	0.238
		Iteration	0.533	1	0.466		
		Treatment × iteration	0.034	1	0.855		
Hormonal	PC1	Treatment	2.806	2	0.246	0.143	0.143
		Iteration	**7.633**	**1**	**0.005**		
		Treatment × iteration	0.405	2	0.817		
	PC2	Treatment	0.901	2	0.637	0.108	0.220
		Iteration	1.837	1	0.175		
		Treatment × iteration	**5.988**	**2**	**0.050**		

Note: Treatments include either direct feeding, fasting, or hormonal manipulations (leptin, ghrelin, or saline). Twenty-three muskellunge in a laboratory setting underwent two behavioral assays with a duration of 5 days between iterations for feeding and fasting assays. Muskellunge were either fasted or fed to satiation with fathead minnows, and the initial assays were conducted on October 8, 2022, and repeat assays were conducted October 13, 2022. Thirty-three muskellunge were assessed within the hormonal assays, with eleven individuals implanted with leptin, grhelin, or saline. Individuals were first anesthetized with 50 mg/L of buffered MS-222, and implanted (via 1 cm incision in the peritoneal cavity) with a micro-osmotic pump (Alzet 1007D micro-osmotic pump from DURECT Corp.) containing either 100 μL of 550 ng/μL of leptin, ghrelin, or 100 μL of a teleost saline solution (10 mL Na_2CO_3/L of 0.6% NaCl). Following a 24 h recovery period, the initial hormone behavioral measurement was conducted on October 13, 2022, and the repeat test was conducted on October 18, 2022. Response variables of the models include behaviors distilled into a PC1 or PC2, which are further described in Table 2. Marginal and conditional r^2 to assess model fit without or with random effects (respectively) are included with each model.

(Biro & Stamps, 2008; Killen et al., 2013). Fish must adjust their behavior and physiology to survive in the wild, because food levels naturally fluctuate (McCue, 2010; Navarro & Gutierrez, 1995), with periods of high or low food availability (Arrington et al., 2002; Vinson & Angradi, 2011). Periods of food deprivation as brief as 2 days are sufficient to change fish behavior (Ali & Wootton, 2001; Ceinos
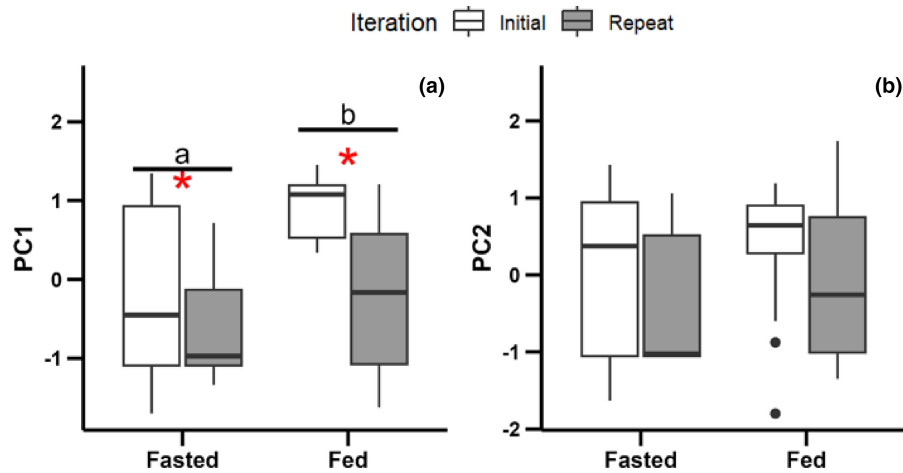
FIGURE 2 Changes in behavioral metrics across treatments and testing sessions: Boxplots showing the changes in behaviors for twenty-three muskellunge in a laboratory setting that underwent two behavioral assays with a duration of 5 days between iterations. Panel a shows how PC1 varied across feeding and fasting (see Table 2 for additional details on PCs), and Panel b visualizes how PC2 varies across feeding and fasting. The white bars represent the initial behavioral assay, which was conducted on October 8, 2022, and the gray bars represent the repeated assay after 5 days which was conducted on October 13, 2022. Significant changes between initial and repeat trials within a treatment are depicted with an asterisk (*), and significant difference between treatments are depicted with a letter. Horizontal lines in boxplots show the median, 25th and 75th percentile values, with whiskers extending up to 1.5×the interquartile range (IQR).
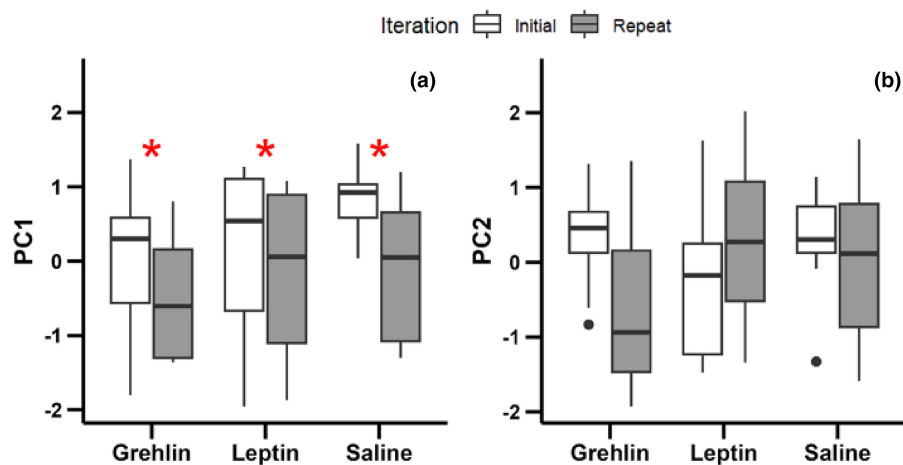

FIGURE 3 Changes in behavioral metrics following hormone manipulations: Boxplots showing the behaviors of thirty-three muskellunge in a laboratory. Individuals were first anesthetized with 50 mg/L of buffered MS-222, and implanted (via a 1 cm incision in the peritoneal cavity) with a micro-osmotic pump (Alzet 1007D micro-osmotic pump from DURECT Corp.) containing either 100 μL of 550 ng/μL of leptin, ghrelin, or 100 μL of a teleost saline solution (10 mL Na_2CO_3/L of 0.6% NaCl).There were 11 fish in each group. Fish recovered for 24 h prior to an initial behavioral assessment conducted on October 13, 2022, and then were returned to tanks for 5 days prior to a repeat behavioral assessment conducted on October 18, 2022. Panel a visualizes how PC1 varied across leptin, ghrelin, and saline treatments (see Table 2 for additional details on PCs). Panel b shows how PC2 varied across hormone treatments. White bars indicate the initial assay, and gray bars indicate the repeated assay following a period of 5 days. Significant changes over time are depicted with an asterisk (*). Horizontal lines in boxplots show the median, 25th and 75th percentile values, with whiskers extending up to 1.5×the interquartile range (IQR).

et al., 2008; Keiling & Suski, 2019; Krause et al., 1999; Laland & Reader, 1999). For example, food deprivation for as little as 4 days led to a 50% increase in activity and aggression in Japanese flounder (*Paralichthys olivaceus*; Miyazaki et al., 2000), presumably because food-deprived fish became more active to seek food. In contrast, for goldfish (*Carassius auratus*), Siberian sturgeon (*Acipenser baerii*), and sterlet (*Acipenser ruthenus*), 1 days of food deprivation led to decreased activity (Zdanovich, 2006), presumably because fish

became less active to conserve energy. The lack of change in behavior following food deprivation we observed may be due to two possible explanations. First, behaviors we measured may not be affected by food availability because of their importance for survival (Killen et al., 2013; Kok et al., 2019). During high stress, such as food deprivation, fish may be unable to change behavior, and behavior relevant to exploration and aggression may offer advantages in acquiring food or avoiding predators (Killen et al., 2013),

TABLE 4 Descriptive statistics for hormones analyzed via ELISA.

Treatment	Leptin concentration (ng/mL)	Leptin SE	Ghrelin concentration (ng/mL)	Ghrelin SE
Leptin	0.408	0.163	–	–
Ghrelin		–	0.600	0.028
Saline	0.335	0.031	0.488	0.020

Note: Thirty-three muskellunge were assessed within the hormonal assays, with 11 individuals implanted with leptin, ghrelin, or saline. Individuals were first anesthetized with 50 mg/L of buffered MS-222, and implanted (via a 1 cm incision in the peritoneal cavity) with a micro-osmotic pump (Alzet 1007D micro-osmotic pump from DURECT Corp.) containing either 100 μL of 550 ng/μL of leptin, ghrelin, or 100 μL of a teleost saline solution (10 mL Na_2CO_3/L of 0.6% NaCl). On October 18, 2022, three fish from each group were selected for a 0.5 mL blood draw from the caudal vessel without anesthetic. The whole blood samples were centrifuged at 1000 g (gravity) for 2 min, plasma was removed with a pipette and samples were flash frozen in liquid nitrogen before being stored at −80°C. Duplicate samples of leptin and ghrelin were assayed using commercially available kits and manufacturer directions (Leptin kit, Enzo life sciences, Catalog #ADI-900-028A, Lot # 02032220, Ghrelin kit, Novus Biologicals, Catalog # NBP2-60645, Lot # 102282203). Samples were measured in the hormonal portion of this study for three muskellunge. Where there is a hyphen (–), this indicates that the respective sample was not assessed in the respective assay.

which may lead to increased fitness or reduced mortality (Careau et al., 2014; Debat & David, 2001; Kok et al., 2019). For example, a high proportion of wild muskellunge have empty stomachs (Andrews et al., 2018; Bozek et al., 1999), perhaps because periods of low food availability occur regularly for this species; therefore, the response of muskellunge to food deprivation may not be pronounced. A second possible explanation for why we did not observe changes in the behavior of muskellunge following food deprivation was that labile behavioral traits may not have been measured. For example, food deprivation can reduce sociability (Aimon et al., 2019; Krause, 1993; Krause et al., 1999), and sociability can increase when fed (Killen et al., 2016), which was not quantified in the current experiment. Regardless of the mechanism, muskellunge experiencing 5 days of food deprivation did not change their boldness, aggression, or exploration behaviors.

Food resources increased the capture of muskellunge by anglers 2.5-times over fish that had forage available in our study, a finding similar to prior angling studies using other fish species in both experimental (Baur et al., 1976; Raat, 1991; Ware, 1972), and wild (Mogensen et al., 2014) conditions. This increased capture may be a result of several factors, such as the internal state of the fish, overlap of the fish with fishing gear, and gear selectivity (Lennox et al., 2017). For example, the capture of muskellunge in a Wisconsin lake increased when populations were fished in specific lunar positions (overhead or underfoot), at dusk, and at lower wind speeds, perhaps because these environmental conditions influenced prey-fish activity that caused muskellunge to be vulnerable to angling (Shaw et al., 2021).

In our study, increased capture of muskellunge in ponds without forage could have been caused by three mechanisms. First, food-deprived muskellunge may have changed their behavior to be more frequently captured (e.g., reduced exploration and aggression) (Bieber et al., 2023), although we did not observe changes in the behavior of muskellunge in the laboratory following food deprivation. Second, fish may reduce their selectivity for prey, which increases their willingness to strike a lure (Lennox et al., 2017). For example, intervals of food deprivation resulted in reduced handling times and reduced size selectivity of prey in the 15-spined stickleback (*Spinachia spinachia*) (Kislalioglu & Gibson, 1976) and Atlantic

salmon (*Salmo salar*) (Reiriz et al., 1998). Food deprivation can lead to an alteration in hormone levels, which can alter prey selectivity and make fish more vulnerable to angling (Lennox et al., 2017). Third, we may have captured more food-deprived muskellunge that were not habituated to small prey-like visual stimuli, unlike fish in ponds with minnows. Fish can habituate to auditory stimuli, visual stimuli, and chemical cues (Barton, 2002; Berejikian et al., 2003; Meliska & Meliska, 1976; Rojas et al., 2021), and can retain and apply knowledge of lures in different settings and presentations (Lovén Wallerius et al., 2020; Takahashi & Masuda, 2021). Therefore, fish can distinguish between closely related stimuli (i.e., a fish to a lure) and apply learned behavior to situations that may explain lower capture rates in ponds with forage. However, the response to stimuli is likely species-specific (Fernandes-de-Castilho et al., 2008; Ferrari et al., 2010; Vilhunen, 2006), and our use of different lures and presentations while angling in ponds were all less effective in ponds with minnows. In conclusion, we do not know the mechanism, but reduced food availability may cause muskellunge to become more vulnerable to angling.

Leptin and ghrelin did not change behavior, such as boldness, exploration, or aggression, in muskellunge in our study, which has previously been shown to cause behavioral changes in fish, such as increased activity, boldness, and risk-taking (Keiling & Suski, 2019; Killen et al., 2011; Stoner, 2003), although these hormones have not been assessed in muskellunge before. In many taxa, including fish, ghrelin is an appetite stimulant (Jönsson et al., 2007; Shepherd et al., 2007), while leptin is an appetite suppressant (Volkoff et al., 2003, Zhang and Chua 2011), so we hypothesized that treating fish with leptin or ghrelin would cause behavioral changes. The concentrations we used (550 μg/L of leptin and ghrelin at a concentration of 1.1 ng/g/h over a period of 5 days) exceeded the concentration of leptin that reduced Atlantic salmon growth by 25% (Murashita et al., 2011). Additionally, a concentration of 150 μg/mL of leptin in goldfish over a period of 2 days led to a 50% reduction in activity (Vivas et al., 2011). The human recombinant leptin and ghrelin used in our study were effective for inducing behavioral changes, including decreased food intake by goldfish and increased food intake by rainbow trout (De Pedro et al., 2006; Matsuda et al., 2012;

Unniappan & Kieffer, 2008; Weil et al., 2003). Further, the pumps used in our study delivered hormones at a constant rate, which likely prevented time-related effects of delivery (Bittner et al., 2000; Hagg, 1994). Levels of leptin and ghrelin in plasma measured at the end of our study were lower than predicted, albeit higher than saline controls and well above the assay sensitivity, but may have failed to induce changes in behavior, or assay kits may have failed to detect hormone levels in plasma. Human-based ELISAs like those used in our study have successfully measured leptin and ghrelin in fish (Audira et al., 2018), although alternate methods may have detected hormones in plasma of fish, such as quantitative polymerase chain reaction (qPCR) (Unniappan & Kieffer, 2008) and radioimmunoassays (RIA) (Hanson et al., 2009; Jönsson et al., 2007). The role of these hormones in fish remains unclear and bears further study (Lin et al., 2000; Volkoff & Peter, 2006; Zhang & Chua, 2011). Future research should assess how hormones influence the angling vulnerability of fish.

We theorize two possible mechanisms to explain why we did not observe increased capture of muskellunge in response to food availability. First, capture rates of muskellunge in ponds may have increased because fish were deprived of food for only 5 days during behavioral testing, whereas angling was after 7–14 days of food deprivation, which rendered food deprivation periods uneven across assays. A 5-days period was selected for food deprivation in the laboratory study based on previous research (Ali & Wootton, 2001; Ceinos et al., 2008; Figueroa et al., 2001). Moreover, a 5-days period between behavioral assays was used to minimize variation in abiotic conditions inherent with outdoor holding that could have confounded behavior (Killen et al., 2016). Different periods for angling and laboratory experiments in our study likely did not cause differences in behavior because behavioral responses were consistent for weeks in earlier studies (Méndez & Wieser, 1993; Meyer et al., 2012). In contrast, animal behavior can differ between lab and wild (Cooke et al., 2002, 2013; Irschick et al., 2005). *For example, aggressive behaviors in agamid lizards (Agama savignyi) occurred only in the laboratory but not in a natural setting* (Hertz et al., 1982; Irschick, 2003). Similarly, boldness-related behaviors of mirror carp (*Cyprinus carpio carpio specularis*) and scaled carp (*Cyprinus carpio carpio haematopterus*) were less pronounced in a pond than in the lab (Klefoth et al., 2012). *Hence, different environments used in our study (pond vs. laboratory) may have led to different behaviors, so results in the laboratory may not translate to those in ponds.*

Our findings have several important implications for the management of muskellunge. First, when managers stock muskellunge into reservoirs, they should also be cognizant of the abundance of potential prey items that could be consumed by muskellunge. For example, in Shabbona Lake, a midwestern reservoir revered for its muskellunge fishing, thousands of potential prey items that could be consumed by muskellunge, including bluegill, largemouth bass, yellow perch (*Perca flavescens*), and walleye (*Sander vitreus*) (Bozek et al., 1999), are stocked annually (Illinois Department of Natural

Resources, 2023). In the scope of the present study, the level of prey available to muskellunge would influence capture, with high prey availability potentially reducing capture by anglers. Second, managers may be able to utilize the relationship between prey availability and angling vulnerability of muskellunge shown in the present study to assist in achieving management goals and address angler satisfaction. More specifically, if managers are interested in a trophy muskellunge fishery with large fish but possibly low catch rates, then an abundance of prey items might help achieve this goal by promoting fish growth. However, if constituents are interested in higher catch rates and possibly trading off these higher catch rates for smaller fish, then a low abundance of prey might help achieve that goal (Ward et al., 2016). Managers concerned about muskellunge catch rates should ensure they have also conducted population assessments for prey fish species rather than focus on a single-species approach (Link et al., 2002). The present work has shown an interplay between muskellunge angling vulnerability and the abundance of prey within a system. As a result, a single-species management approach to muskellunge fisheries may make it less likely to achieve management goals, and an ecosystem approach to management should be considered (Ward et al., 2016). An ecosystem approach to management can better define the relationship between the environment and target species, inform recreational fishery management outcomes, and facilitate a successful muskellunge fishery.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Illinois Databank at https://doi.org/10.13012/B2IDB-8452275_V1.

ETHICS STATEMENT

All experiments were conducted with the approval of the University of Illinois with Institutional Animal Care and Use Committee, protocol # 20165.

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