Canadian Journal of Fisheries and Aquatic Sciences

OPEN ACCESS | Article

Effects of behavioral strategies on catchability, bait selectivity, and hunting behavior in northern pike (*Esox lucius*)

Jorrit Lucas[a], **Albert Ros**[a], **Juergen Geist**[b], **and Alexander Brinker**[a,c]

[a]Fisheries Research Station Baden-Württemberg, LAZBW, Langenargen D-88085, Germany; [b]Aquatic Systems Biology Unit, Department of Life Science Systems, TUM School of Life Sciences, Technical University of Munich, Freising D-85354, Germany; [c]University of Konstanz, Mainaustraße 252, Konstanz D-78464, Germany

Corresponding author: **Jorrit Lucas** (email: jorrit.lucas@lazbw.bwl.de)

Abstract

This study investigated how northern pike with two behavioral strategies in the context of predation interact with natural and artificial baits in simulated angling experiments. Predator types were assessed in three behavioral trials over 15 days by measuring foraging latency under altered conditions (abruptly increased light intensity). Latency revealed fast and slow predator responses showing high individual repeatability, interpreted as proactive and reactive predator types, with reactive individuals adapting their response over time. Both types displayed similar hunting performances in predation trials with live prey under habituated conditions. In angling trials, proactive pike expressed significantly more predation than reactive pike, independent of bait type. During angling trials, predator type did not affect bait handling, while both predator types developed strong sequential bait avoidance, indicating a learning effect. Angling trials did not affect hunting for live prey. The results suggest that pike exhibit individual differences in responses to environmental changes linked to their predatory behavior. Angling selection may play a role in pike populations, with the proactive predator type more likely to be hooked than the reactive type.

Key words: learning, fishery-induced selection, apex predators, lures, recreational angling

Introduction

Behavior is a plastic trait that enables animals to acquire adaptive responses to their changing environments (Sih et al. 2011). However, it has become increasingly clear that animals exhibit intricate behavioral phenotypes that are remarkably stable over time and across various contexts (Sih et al. 2004; Bell 2007; Keenleyside 2012; Kalueff et al. 2013), and which may be the outcome of heritable (Brown et al. 2007; Réale et al. 2007), environmental (Dingemanse et al. 2009), and maternal effect (Laskowski et al. 2022) components. These behavioral phenotypes encompass the expression of higher-order behavioral outcomes such as feeding, territorial, and mating strategies and thereby affect life-history traits like growth, survival, and reproduction in a wide range of species (Wolf and Weissing 2012), including those of fish (Toms et al. 2010; Conrad et al. 2011; Castanheira et al. 2013). From this background the question was raised whether fishes with different behavioral strategies respond differently to anthropogenic disturbances, e.g., human activities like fishing (Coltman et al. 2003; Smith and Blumstein 2013; Diaz Pauli and Sih 2017). Fishing has been shown to potentially generate selective effects on morphological traits, e.g., through the use of size-selective fishing gear or through angler preferences to capture fish of large size (Coble 1988; Heino and Godø 2002; Carlson et al. 2007). As a consequence, fishing may lead to evolutionary effects over time, like earlier maturing fish at smaller sizes (Swain et al. 2007; Anderson et al. 2008; Alós et al. 2014; Heino et al. 2015). Similarly, fishing could directly affect fish populations through the selective removal of individuals with behavioral strategies that make them more vulnerable to a common capture method (Biro and Post 2008; Uusi-Heikkilä et al. 2008; Wilson et al. 2011; Alós et al. 2012; Arlinghaus et al. 2017*b*; Monk et al. 2021).

Selective removal of fish based on their behavior may be a common side effect of recreational fishing targeting specific foraging behaviors (Nannini et al. 2011). For example, some studies have already shown that passive fishing gear can unintentionally target bolder, more aggressive, and/or more active individuals, potentially removing significant portions of behavioral variation from these populations (Olsen et al. 2012; Mittelbach et al. 2014; Philipp et al. 2015; Monk et al. 2021; Bieber et al. 2023). Angling trials were conducted with several species important to recreational fisheries; for example, in rainbow trout (*Oncorhynchus mykiss*), more bold and faster-growing fish were caught more frequently than slow-

moving, shyer individuals (Biro and Post 2008) as were more active and stress-resistant individuals (Koeck et al. 2019). In common carp (*Cyprinus carpio*), bold and active fish are more likely to be caught by angling (Klefoth et al. 2017). In largemouth bass (*Micropterus salmoides*), negative selection pressure was found on male individuals showing aggressive behavior toward fishing lures while showing territorial defense of their nest (Suski and Philipp 2004; Philipp et al. 2009; Sutter et al. 2012). Interestingly, the nonexploratory and nonaggressive individuals can also be selectively targeted by angling, as was shown in muskellunge (*Esox masquinongy*) (Bieber et al. 2023). It has even been found that by applying small changes in gear types or techniques, for example, different types of bait, individuals of different personalities within a population can be targeted (Wilson et al. 2015; Härkönen et al. 2016).

Selective fishing techniques targeting fish with specific behavioral strategies might result in a decrease in the diversity of behavioral phenotypes in the fished population. One of the reasons for such a decrease in behavioral phenotypes might be through learning in released individuals and/or social learning from other individuals, which contributes to behavioral plasticity effects (Askey et al. 2006; Louison et al. 2019; Koeck et al. 2020; Lovén Wallerius et al. 2020). Therefore, susceptibility to capture not only depends on the fish's behavior but also on its motivation (hunger state), frequency of encounter with fishing gear, the specific characteristics of the gear, and learning (Beukema 1970; Lennox et al. 2017; Arlinghaus et al. 2017*a*). Finally, selection based on behavioral strategies might have negative consequences for the overall fitness and resilience of stocks (Arlinghaus et al. 2017*b*). Hence, it is important to monitor fishing impacts not only in terms of fish numbers but also in terms of the variation in behavioral phenotypes.

The northern pike (*Esox lucius*), hereafter referred to as pike, is one of the most popular target species for recreational anglers fishing in freshwater and low salinity brackish waters of the northern hemisphere due to its potential large size and vigorous predatory behavior (Arlinghaus et al. 2008, 2021; Dorow and Arlinghaus 2011). As pike are apex predators, they play an essential ecological role in structuring fish populations at lower trophic levels (Nilsson and Brönmark 2000; Mehner et al. 2004; Craig 2008; Nilsson et al. 2019). Due to their natural tendency to attack prey from ambush (Harper and Blake 1991; Říha et al. 2021), pike are also highly susceptible to angling pressure compared with other species in the same water body, as spots with underwater vegetation as preferred habitat for pike are easily identified by anglers (Grimm and Klinge 1996; Klefoth et al. 2008). The high angling pressure is thought to have changed the size distribution of pike in many populations, with large individuals being preferentially targeted by anglers (Pierce et al. 1995; Post et al. 2002; Arlinghaus et al. 2010; Pierce 2010). If such high angling pressure would also target individuals expressing a specific behavioral strategy, this would result in additional changes in pike populations with still unknown consequences for future pike catchability and possibly even for the aquatic ecosystem.

There are some indications for variation in behavioral phenotypes in the natural hunting behavior of pike. For example, field studies have shown individual differences in habitat use, movement range, and general activity (Kobler et al. 2009; Amalie 2018; Røste 2020). More active pike have been shown to be more likely to be caught by angling than less active pike, presumably due to the likelihood of encountering a bait (Monk et al. 2021). Part of this variation is environmentally modulated (Kuparinen et al. 2010; Öhlund et al. 2015) and acquired by learning (Beukema 1970; Arlinghaus et al. 2017*a*). For example, Beukema (1970) showed evidence of learned avoidance toward fishing lures and baits, where pike repeatedly preferred a live fish bait over an artificial lure. From this wide range of studies, it seems highly likely that intensive angling through learning and selective mechanisms constitutes a driver capable of altering life history and behavioral traits in exploited populations (Arlinghaus et al. 2009*b*; Chang et al. 2017; Monk et al. 2021).

The range of baits available to anglers targeting predatory fish has grown exponentially, from mainly natural options like dead bait fish to an increasing variety of artificial lures, of which soft plastic options are currently very popular among anglers (Raison et al. 2014; Arlinghaus et al. 2017*a*). Studies on the influence of spatial encounters and lure type on pike catchability showed that pike more often respond to plastic lures than artificial metal spoons (Arlinghaus et al. 2017*a*). There is evidence that soft plastic lures are swallowed deeper than other artificial baits (Arlinghaus et al. 2008, 2017*a*; Stålhammar et al. 2014). Whether pike show differences between the handling of natural baits and artificial lures has not been scientifically studied yet.

The central hypothesis of the study is that consistent variation in predator behavior of the northern pike exists and that such variation in behavioral strategies has consequences for vulnerability to angling. A 3D camera setup was used with the following aims: (i) to test for consistency in the individual behavioral response. As is customary in studies of behavioral syndromes (e.g., coping styles, personalities; Koolhaas et al. 1999; Réale et al. 2010), this consistency in behavioral responses was tested under abruptly and temporarily altered environmental conditions in a standardized setup (three replicates, increased light intensity, and placement of an acrylic tube). To study the possible consequences of angling on different behavioral strategies in pike, the following questions were asked: (ii) how do pike of different predator types respond to different fishing baits (a soft plastic natural colored lure, a soft plastic bright colored lure, and a natural dead bait fish)? (iii) do pike expressing these behavioral strategies handle bait and lure types differently, and (iv) is the natural hunting behavior of these pike targeting natural prey modified after experience with a fishing bait? Pike predator types were inferred from the latency to attack measured from the repeated standardized tests (i). In these tests, live prey in a transparent tube was presented to the pike under an abrupt temporal change in environmental conditions (increased light intensity and placement of the acrylic tube). It was then analyzed how these differences in predator types related to feeding behavior under habituated conditions (iv) and the responses to different lure types (ii and iii).

Materials and methods

Ethics approval

All trials were conducted according to the German Animal Welfare Act (TierSchG), and ethical permission was granted by the appropriate regional authority responsible for animal experimentation administration, the Regierungspräsidium Tübingen, Referat Tierschutz (animal experiment application: LAZ 01/20G). In order to study pike predator behavior, permission was granted for foraging trials with live prey. These trials were continuously monitored, and in case the prey was not directly swallowed after being attacked, it was taken out of the aquarium and killed immediately by a cardiac stab according to the German Animal Protection Law (§4) and the ordinance of slaughter and killing of animals (Tierschlachtverordnung §13). Adult pike for rearing (see 2.3) were caught according to the current fishery law (LFischVO) under the permission of the local fisheries administration (RP Tübingen).

Study concept

The experimental setup was derived from literature suggesting that there is a difference between individuals in how fast they cope with changes in their environment, with one group of individuals being insensitive or habituating fast to the changes, quickly returning to "routine-like" responses (fast copers, risk-taking), whereas another group of individuals takes a longer time to adjust to the altered conditions (slow copers, risk-averse) (Koolhaas et al. 1999; Coppens et al. 2010). For example, faster animals show bolder, in this case more risk-taking behavior after a stressor has been applied (willingness to search for food after a predator attack; Bell 2005), and faster/bolder animals show shorter latency when leaving shelter to forage in an open area (Brown et al. 2005; Harcourt et al. 2009). In the current experiment, an abrupt temporary increase in light intensity was applied as an environmental change (stressor) to test for fast (proactive) and slow (reactive) predator types. Increased light intensity is known to induce behavioral changes such as increased wariness (Tian et al. 2015; Laskowski et al. 2016; Moltesen et al. 2016) and surface avoidance behavior (Endler 1987) and to modulate the hypothalamus-pituitary-interrenal axis involved in the fish's stress responsiveness (Lee et al. 2019). Furthermore, the placement of the acrylic tube at the start of these trials is thought to act as an additional stressor. The experiment was limited to predator behavior, and thus no inference was made as to whether the results would fit in a personality context, as behavioral consistency was not measured over different contexts. Therefore, further individual differences in behavioral phenotypes are referred to as "behavioral strategies" of "predator types" and refer to the actual behavioral measurement, i.e., latency to forage under temporarily altered conditions.

Origin of experimental animals and holding conditions

To minimize sampling bias in the pike used for the experiments and to ensure that the fish had never encountered fishing baits before and shared the same life experiences, pike were bred and raised from eggs of wild-caught pike in a highly controlled laboratory environment. The parent pike were caught with fyke-nets during a regular spawning fishery in February/March 2019 from a lake with historically little to no fishing pressure in southern Germany, the 22 ha "Ruschweiler See" (47°52′12.6″N 9°21′57.4″E). More than 10 males and 10 females were stripped, and fertilized eggs were transferred to a nearby small-scale hatchery. The eggs were kept in hatching jars under flow-through conditions, and once the fry had hatched, they were transferred into rectangular troughs until they were free-swimming. At that stage, they were transferred to the "Fischbrutanstalt Reichenau", a hatchery located on Lower Lake Constance. Once they started feeding, they were supplied ad libitum with plankton collected from the lake. After reaching a size of 2.5–3 cm at the end of April 2019, they were transferred again to the Fisheries Research Station in Langenargen. For further holding conditions, see Supplement.

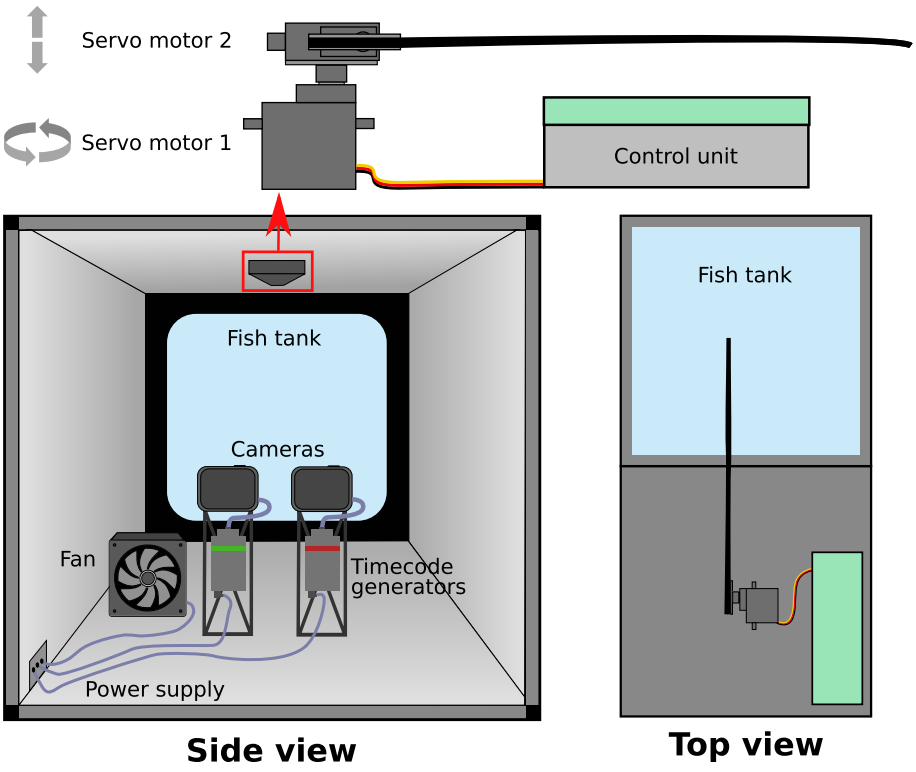
Experiments were conducted from July to October 2020. Two weeks before the start of the trials, 12 pike at a time were transferred from their holding tanks, and each was assigned to a numbered 120 L water tank (50 × 50 × 50 cm). Experimental fish had no visual contact with other individuals. All tanks were in the same room and connected to a partially recirculating aquarium system that received clear running water originating from Lake Constance. Lighting conditions were 12 h/12 h (for details, see Supplement). The light intensity measured (Illuminance Meter T-10A, Konica Minolta, Inc., Japan) in the center of these tanks (at 25 cm of depth) was 420 lx. Living brown trout (*Salmo trutta*) were supplied as prey and introduced to random locations within the tank to prevent habituation of the pike to a particular feeding spot. Brown trout are a natural prey of pike (Öhlund et al. 2015) and these fish were obtained from a local hatchery.

Camera setup and 3D calibration

A mobile stereo camera setup was installed successively in front of each of the 12 experimental tanks using two GoPro Hero 8 cameras (firmware: v2.50) (Fig. 1). This made it possible to record the behavior of the pike in 3D space without human interference. The distance between the centers of the lenses of the cameras was 11 cm, and the distance of the cameras to the tank was 30 cm (Fig. 1). The cameras were mounted parallel to each other in an aluminum frame. Their lenses faced each other at an angle of 5°: the left camera was aligned at an angle of 95° to the tank, and the right camera at an angle of 85°. The frame around the cameras was covered with opaque fabric to prevent movement in the room from interfering with the experiment. A fan was used to prevent fogging of the glass. Frame-by-frame synchronization was achieved by means of a time code generator (Tentacle Sync E; Tentacle Sync GmbH, v.2.0) that transmitted a time code to one channel of the audio track of both camera recordings. A mobile battery (Anker PowerCore 26800 mAh) was used as a power supply for the cameras.

3D camera calibration and tracking were performed using the open-source software "Argus::3D for the people" (v.2.1)

Fig. 1. Front view of the experimental 3D camera setup for all experiments in front of one of the experimental tanks (left); top view of a mechanically operated angling rod controlled by two servos and an Arduino UNO board installed on top of the camera setup (right).



and "DLTdv digitizing tool" (v.8.2.3) (Hedrick 2008; Shams et al. 2019). Intrinsic camera parameters, including focal length and optical center, were captured using the Argus-Patterns function with a 9 × 12-dot grid pattern, a dot spacing of 2 cm, and a dot diameter of 1 cm, recorded from within the aquarium. The 3D coordinates of the cameras were converted to 2D image coordinates by using the dot grid pattern and then calculated using the Argus-Calibrate function. The Argus-Wand function was used to calibrate extrinsic parameters, such as the orientation of the cameras in the 3D environment. For calibration, a two-point wand with a dot diameter of 1 cm and a center point distance of 10 cm was recorded simultaneously with both cameras while moving in a filled aquarium. The points were tracked automatically using the DLTdv digitizing tool and imported into Argus-Wand along with the previously calibrated intrinsic parameters to complete the calibration of the cameras. To minimize errors caused by accidental movement of one of the cameras before or during the experiment, the recording was repeated for stereo calibration before each trial. The calibration error was checked by analyzing wand tracks (points spaced 10 cm apart). The accuracy of the 3D calibration should correspond to an error of <1 cm·m^{-1} (Letessier et al. 2015). The result was a mean estimated distance of 10 cm (N = 3042, 95% CI ± 0.01 cm), confirming the calibration as accurate.

Experimental setup

Each pike was tested eight times over a 15-day experimental period, with a 24-hour break between tests. Pike were fed after each test to create standardized conditions for each individual. The total length of each individual was measured digitally from a side view using the calibrated 3D camera setup to adjust the prey and bait sizes accordingly. For all trials, the mobile camera system was installed in front of the viewing window 15 min before the start to allow habituation. Details on additional repeat recording, handling, and analysis methods can be found in Table 1. For details on the video analysis, see the Supplement. Pike were tested in four batches (N = 12, 12, 12, 6). At the end of each experimental period, the tested individuals were anesthetized with clove oil, measured (TL in cm to the closest 0.1 cm), and weighed (g to the closest 0.1 g). Subsequently, the animals were released in a suitable habitat according to experimental permissions, and the next 12 pike were transferred into the testing tanks, and the process continued until all 42 pike were tested (N = 42, total length [TL] = 22.7 cm, SD = 2.5, body weight [BW] = 70.1 g, SD = 22.4).

For each pike, the order of trials was B P B A A A P B, with B = behavioral trial, P = predation trial, and A = angling trial.

Behavioral trials

For each pike, attack latency was measured in a standardized behavioral trial. At the start of each trial, an acrylic tube (47.5 cm height, Ø = 10 cm) closed at the bottom was placed in the center of the tank. After the 15 min acclimation period, three live brown trout with an average total length of ca. 25% that of the pike were gently placed in the cylinder. To

Table 1. Summary of repeated recording, handling, and analysis methods for the experiments with pike.

Trial type	Behavioral trial	Angling trial	Predation trial
Camera settings	GoPro linear mode at 30 FPS	GoPro linear mode at 60 FPS	GoPro linear mode at 60 FPS
Light intensity	80% light increase (760 lx)	Normal light conditions (420 lx)	Normal light conditions (420 lx)
Acclimation time	15 min, recording started 5 min before trial start	15 min, recording started 5 min before trial start	15 min, recording started 5 min before trial start
Stimulus	Three living brown trout	One mechanically moved fishing bait	One living brown trout
Analysis start	First frame in which the first trout entered the cylinder	First frame in which the pike orients toward the bait	First frame in which the pike orients toward the trout
Analysis stop	First completed snapping movement toward trout	First completed snapping movement toward bait	First completed snapping movement toward trout
Maximum trial duration	25 min or until snap at trout	15 min or until strike at bait	15 min or until strike at trout
Variables measured	Latency to attack any trout (seconds)	• Occurrence of attack (yes/no) • Distance orientation (cm): distance between pike and bait during orientation toward bait • Distance attack (cm): distance between pike and bait before final acceleration of the pike • Maximum speed ($cm \cdot s^{-1}$): max. velocity of pike during the attack • Handling of the different baits on capture (ingestion/rejection)	• Occurrence of attack (yes/no) • Distance orientation (cm): distance between pike and trout during orientation toward prey • Distance attack (cm): distance between pike and trout before final acceleration of the pike • Maximum speed ($cm \cdot s^{-1}$): max. velocity of pike during the attack
Subsequent treatment	Feeding with living brown trout, no other test challenges for 24 hours	Feeding with living brown trout, no other test challenges for 24 h	Feeding with living brown trout, no other test challenges for 24 h
Tracking points	No tracking	Pike: center of the head; bait: eye/corresponding spot in the front of the lure	Pike: center of the head; trout: eye
Software	• VLC Media player: screening for events • DLTdv digitizing tool: identification of frame numbers	• VLC Media player: screening for events • DLTdv digitizing tool: identification of frame numbers and 3D tracking	• VLC Media player: screening for events • DLTdv digitizing tool: identification of frame numbers and 3D tracking

provide chemical cues for both pike and brown trout, small holes at the bottom of the cylinder provided an inlet for ambient water. The attack latency from the placement of the trout until the first strike by the pike was measured in seconds. The pike were given a 25 min period to react to the trout in each trial.

During each behavioral trial, light intensity was abruptly increased by 80% from the habituated 420 lx to about 760 lx to apply a stressor in the form of an abrupt and temporary change in environmental conditions (in addition to the placement of the acrylic tube) (see, for example, Ryu et al. 2020). To assess individual consistency, three behavioral trials were conducted for each animal: one at the beginning of the experiment, one in the middle of the experimental period, and one at the end of the experiment.

Predation trials

Two trials were recorded for each pike, using living brown trout as prey. The aim of these trials was to describe the hunting behavior of the pike under habituated conditions and to compare whether this hunting behavior of the pike changed from before to after the angling trials in connection with their predator type derived from the behavioral trials. One trial was recorded at the beginning of the experimental period, the second at the end of the experiment. After the pike had acclimated to the camera setup, one live brown trout with an average length ca. 25% that of the pike was gently placed in the upper right corner of the tank, and the pike was given 15 min to react to the prey. Parameters recorded were as follows (Table 1): (1) the distance of the pike when it oriented to the prey, with orientation defined as the first movement resulting in a clearly observable focus on the prey; (2) the distance of the pike before the attack, with the starting point taken as the distance at which the pike began its final acceleration before striking at the prey; and (3) the mean maximum speed reached by the pike, calculated as an average of the three highest values observed during the final acceleration before a strike.

Angling trials

Three trials per pike were carried out in the middle of the experimentation period. The baits chosen for these trials were natural bait and two types of soft plastic lures, one with natural prey-fish coloration and one with bright coloration. No hooks were used. The natural bait was a dead brown trout that had been frozen fresh and thawed shortly before use. The artificial bait was a Relax brand "Bass 2.5" type rubber shad bait with a length of 7 cm.

The type BAS25-L179 (clear-silver glitter, Carolina pumpkin-black, red glitter) was selected as the natural color lure, and the type BAS25-L632 (chartreuse-orange, black glitter, orange-silver glitter) was selected as the bright color (Fig. 2). The artificial baits did not contain any salts or scents as attractants.

To ensure that all artificial and natural bait types performed the same movements for each pike, a mechanically operated fishing rod was constructed and controlled by a programmed Arduino board (Arduino UNO v.1.8.15) and two 180°-servos (SUNFOUNDER 55 g, stall torque 13.5 kg) controlling vertical and horizontal movement, respectively, attached to the top of the camera installation. The fishing rod consisted of a 25 cm carbon fiber tip with 25 cm of 0.12 mm fluorocarbon line (Stroft, FC1, 1.5 kg) attached. A split shot weight (Decoy, 0.6 g) was fitted in front of the bait. The end of the line was connected to a round snap (Decoy, size #000) and the lure was attached to the snap by means of a lure keeper (Gurza, size ULS), which was screwed into the head of the bait (for the schematic and Arduino code, see Supplement). The fishing rod moved in such a way that a vertical rectangle was drawn in the aquarium (right, stop, right, down, up, down, left stop, left, up, down, up). Every pike was tested once with each bait in a randomized order, and baits were replaced for each pike. After the fish had acclimated to the camera setup, the bait was placed in the upper left corner of the tank, and the pike was given a 15 min period to react. To ensure consistency, the bait size was matched to the pike size by selecting appropriately sized frozen trout or trimming of head section of the soft plastic bait. Pike longer than 23 cm were tested with a 7 cm bait ($N = 22$), and those shorter than 23 cm were tested with a 5 cm bait ($N = 20$), resulting in a consistent mean bait size of 26.5% ± 0.8% of pike length ($N = 42$; 95% CI). None of the pike cut the line after capturing the bait.

The same parameters were recorded for the angling trials as for the predation trials (see Table 1). In the statistical analysis of these trials, the focus was placed on whether a pike attacked the bait or not within the 15 min time frame. Additionally, it was noted how the pike handled each of the different baits on capture (ingestion/rejection).

Data analysis and statistical methods

Behavioral trials

The classification of pike predator types was carried out using a *k*-means cluster analysis. The consistency of predator type assignment over the three trials was assessed using a Naïve Bayes analysis for each trial. Repeatability (*R*) of individual willingness to forage over the three periods was calculated using the R package rptR as the ratio among individual variance and the sum of variances (Nakagawa and Schielzeth 2010; Wilson 2018). Fulton's body condition factor K (Nash et al. 2006) was used to test for condition differences between predator-type clusters. The estimate was corrected using the allometric relationship between total length and weight (Ricker 1975) by estimating the exponential factor based on the data of the fast-responding individuals only, resulting in $b = 3.02$ ($N = 28$, $p < 0.001$). Fulton's corrected condition factor K' was then calculated as follows (Le Cren 1951):

$$K' = C \times \frac{\text{Weight}}{\text{Length}^b} \quad (1)$$

in which $C = 100$.

Differences in growth parameters and the corrected body condition factor between groups of predator types were then tested with Student's *t*-tests. Additionally, linear mixed model (LMM; lmer, R packages lme4; Bates et al. 2015) with individuals as random factors was used to test for changes in latency of attack over the three trials.

Angling trials

To find out which variables in the angling trials were responsible for the pike attacking the bait, a logistic regression (generalized linear mixed model (GLMM) with binomial family and a logit link and individual as random factor, R package lme4) was used according to the following formula:

$$\log\left[\frac{Pa}{1-Pa}\right] = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_1 X_3 + \beta_6 X_2 X_3 + \epsilon_i \quad (2)$$

where Pa is the probability of attack, X_1 is the predator type, X_2 is the bait type, X_3 is the sequential trial order, X_1X_2 is the interaction between predator type and bait type, X_1X_3 is the interaction between predator type and sequential trial order, X_2X_3 is the interaction between bait type and sequential trial order, ϵ_i is the random residual error (individual as random factor), β_0 is the coefficient of the intercept, and $\beta_1 \ldots \beta_6$ are the corresponding model coefficients

Factors influencing the performance parameters of the pike in the angling trials (distance between pike and bait at the beginning of the orientation of the pike (cm), distance between pike and bait at the beginning of the last acceleration before the snap of the pike (cm), and maximum velocity during the last acceleration before the snap ($cm \cdot s^{-1}$)) were determined using separate LMMs (lmer with individual as random factor, R package lme4) according to the following formula:

$$y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_1 X_3 + \beta_6 X_2 X_3 + \epsilon_i \quad (3)$$

where X_1 is the predator type, X_2 is the bait type, X_3 is the sequential trial order, X_1X_2 is the interaction between predator type and bait type, X_1X_3 is the interaction between predator type and sequential trial order, X_2X_3 is the interaction between bait type and sequential trial order, ϵ_i is the random residual error (individual as random factor), β_0 is the coefficient of the intercept, and $\beta_1 \ldots \beta_6$ are the corresponding model coefficients.

How pike handled the different baits on capture (ingestion/rejection) was analyzed using Chi-square tests followed

Fig. 2. Standardized baits used during the angling experiments: (*a*) dead brown trout, (*b*) natural-colored soft plastic lure, and (*c*) brightly colored soft plastic lure.

by sequential Bonferroni adjustment of the *p*-values (Holm 1979).

Predation trials

The parameters collected in the two predation trials were analyzed with the aim of comparing whether the hunting behavior of the pike under habituated conditions changed from before to after the angling trials in connection with their predator type derived from the behavioral trials. Separate LMM (lmer with individual as random factor, R package lme4) were used to detect effects of time (before or after the angling experiments) or predator type in any of three performance measures (distance at orientation, distance at attack, and maximum speed) according to the following formula:

$$(4) \quad y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \in_i$$

where X_1 is the predator type, X_2 is the time (trial before and after the angling experiments), X_1X_2 is the interaction between predator type and time, ϵ_i is the random residual error (individual as random factor), β_0 is the coefficient of the intercept, and $\beta_1 \ldots \beta_3$ are the corresponding model coefficients.

To furthermore identify differences in these performance parameters between predation and angling trials, separate LMMs (lmer with individual as random factor, R package lme4) were used according to the following formula:

$$(5) \quad y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \in_i$$

where X_1 is the predator type, X_2 is the trial type, X_1X_2 is the interaction between predator type and trial type, ϵ_i is the random residual error (individual as random factor), β_0 is the coefficient of the intercept, and $\beta_1 \ldots \beta_3$ are the corresponding model coefficients.

The overall effects of predator type on predation success (within trials) were tested using Fisher's exact test.

Changes in predation over the first and second trials between predator types were tested using logistic regression (GLMM with a binomial family and a logit link, and individual as a random factor; R package lmer4).

Statistical analysis was conducted with the software JMP Pro (version 14.3.0 64-bit; SAS Institute, Cary, NC, USA) and R (version 4.0; R Foundation for Statistical Computing, Vienna, Austria, 2020). Figures were created in Origin 2017 (version b9.4.2.380, 64-bit; OriginLab Corporation, Northampton, MA, USA). All variables are reported as the arithmetic mean ± standard deviation. To correct *p*-statistics for repeated measures per variable, pike individual was added as a random factor to the GLMMs and LMMs (Arnqvist 2020).

Results

Predator types of pike

Cluster analysis resulted in an optimal cluster size of two groups (optimal cubic cluster criterion = 0.59), comprising pike exhibiting long (95% of the attacks occurred after 10 min) and short attack latencies (95% of the attacks occurred within 2 min) under altered environmental conditions. Based on this analysis, 14 pike were classified as slow responders and 28 pike as fast responders (Figures S1 and S2 and Table 2). Naïve Bayes analysis revealed a low misclassification of 7% (Trial 1), 2% (Trial 2), and 23% (Trial 3). Overall repeatability (*R*) of attack latency (in s scaled using $\log_{10}$) over three behavioral trials was 0.51. Measured within each cluster of fast and slow responders, the repeatability of this measure was <0.01.

Fast- and slow-responding pike did not differ statistically in length, weight, or condition (Table 2; *t*-test, $p > 0.05$). Attack latency tended to decrease in slow-responding pike, whereas no statistically significant changes were detected in attack latency in fast-responding pike (Table 2; LMR with individual as random factor: slow responding, $F_{[2,26]} = 5.96$, $p < 0.01$; fast responding, $F_{[2,54]} = 2.68$, $p = 0.08$).

Simulated angling

A logistic regression (GLMM) with individual as a random factor was used for testing which factors (predator type, bait type, and trial order) determine the likelihood of pike attacks (two levels: yes, no) (126 observations, overall significance $X^2 = 37.7$, df = 19, $p = 0.0065$). The factors predator type ($X^2 = 4.72$, $p = 0.030$) and trial order ($X^2 = 7.66$, $p = 0.022$) significantly influenced the probability of attack (Table 3), with slow-responding pike being less likely to snap at the bait compared to fast-responding conspecifics and attack probability decreasing with sequential trial order (Fig. 3). Bait type did not have significant effects on the probability of attack during the trials ($p > 0.05$; Table 3 and Fig. 3).

Pike that were successful in capturing the bait showed clear differences in the handling of the bait types. Natural

Table 2. Tabulation of attack latency (for trials 1 and 2 before, and trial 3 after the angling experiment), total length (TL), body weight (BW), and corrected Fulton's condition factor (Condition *K'*) per group of predator type.

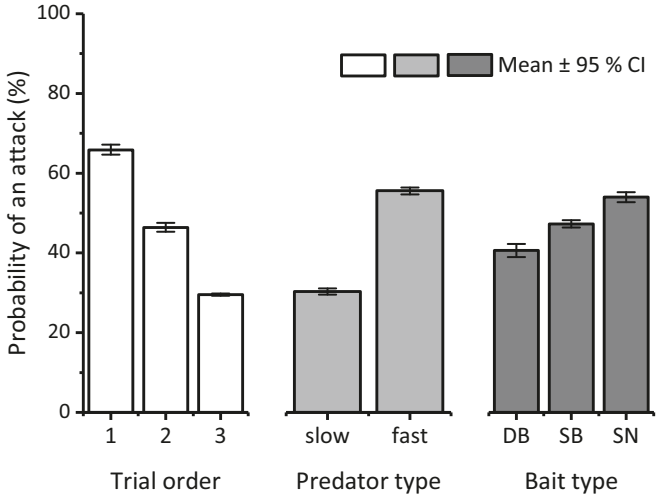
		Latency to attack			Morphometric parameters		
	N	Trial 1 (s)	Trial 2 (s)	Trial 3 (s)	TL (cm)	BW (g)	Condition (*K'*)
Reactive predator type	14	1158 ± 530	706 ± 597	504 ± 594	23.1 ± 2.6	73.0 ± 23.3	0.54 ± 0.04
Proactive predator type	28	74 ± 283	15 ± 47	94 ± 286	22.6 ± 2.5	68.7 ± 22.2	0.54 ± 0.03

Note: Means ± standard deviations are given. For the behavioral trials, three brown trout were placed in a cylinder in the aquarium under increased light intensity.

Table 3. Results of the logistic regression (GLMM) with individuals as random factors determining the variables that influence the probability of an attack on bait in the angling experiments (observations = 126).

Variable	df	X^2	*p*-Value
Predator type	1	4.72	0.030
Trial order	2	7.66	0.022
Bait type	2	2.58	0.278
Predator type × trial order	2	6.56	0.037
Trial order × bait type	4	2.27	0.686
Predator type × bait type	2	0.44	0.801

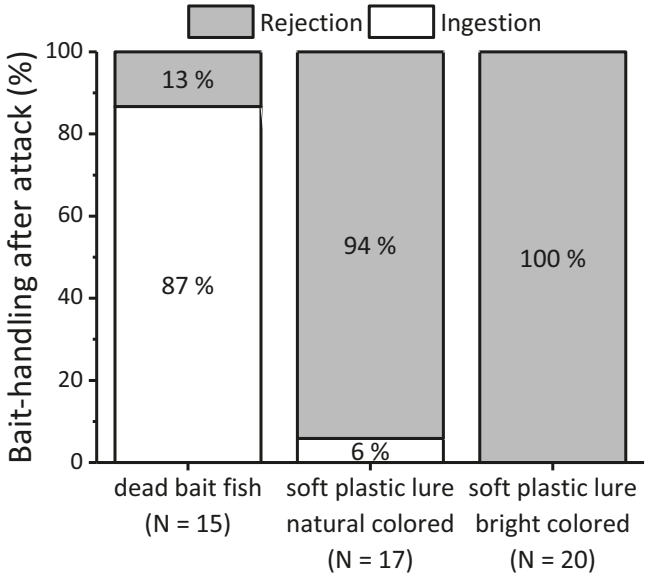
Fig. 3. Marginal means including 95% CI of the logistic regression presenting the likelihood of an attack during the angling trials. Plotted are the variables trial order, predator type, and bait type (dead bait fish, soft plastic lure bright, and soft plastic lure natural).



dead baits were ingested significantly more often than either of the two lure types (natural bait vs. natural colored lure: sequentially Bonferroni-corrected Chi-square tests, $N = 35$, $X^2 = 27.6$, $p < 0.001$; natural bait vs. brightly colored lure: $N = 32$, $X^2 = 21.1$, $p < 0.001$). Both soft plastic lures were rejected on more than 94% of capture occasions (Fig. 4). Bait handling did not differ between predator types (Chi-square tests per bait type: $X^2 < 0.073$, $p > 0.05$).

Pike started orienting toward the bait at an average distance of 22.9 ± 8.5 cm (orientation distance, $N = 106$), launched their attack from an average distance of

Fig. 4. Handling results of the three bait types during successful attacks in the angling experiments (observations = 52). Rejection signifies that the bait was captured but released again.



11.7 ± 4.4 cm (distance of attack, $N = 56$), and reached an average maximum speed of 158.8 ± 42.4 cm·s^{-1} (maximum speed, [body length (BL)/s]: 7.03 ± 2.00, $N = 56$) before striking at the bait. Differences in these three performance parameters were tested using LMM (lmer, R package lme4) with predator type, trial order, and bait type as explanatory variables and individuals as random factors. None of these variables showed a significant effect in the LMMs (overall model significance; orientation distance of the pike toward the bait: $N = 42$, observations = 106, $r^2_{adj.} = 0.16$, $X^2 = 14.15$, df = 13, $p = 0.36$; distance of attack: $N = 33$, observations = 56, $r^2_{adj.} = 0.28$, $X^2 = 15.18$, df = 13, $p = 0.30$; maximum speed: $N = 33$, observations = 56, $r^2_{adj.} = 0.16$, $X^2 = 8.65$, df = 13, $p = 0.80$)

Predation on natural prey

In the predation experiments on natural prey (trial 1 = before and trial 2 = after the angling experiments), all 28 fast-responding pike attacked their prey in every trial, whereas of the 14 slow-responding pike, 10 (71%) attacked their prey in the first trial and 11 (79%) attacked their prey in the second trial, resulting in a significant difference in the number of attacks between predator-type clusters (Fisher exact test, trial 1: $p = 0.009$; trial 2: $p = 0.031$).

No significant individual changes in predation between both trials were found (logistic regression, factor trial $X^2 = 0.19$, df $= 1$, $p = 0.66$; interaction trial with predator type: trial $X^2 < 0.01$, df $= 1$, $p = 0.98$).

Pike started orienting toward live brown trout from an average distance of 29.9 ± 11.8 cm ($N = 81$), launched attacks from an average distance of 12.7 ± 5.6 cm ($N = 77$), and reached an average maximum speed of 164.9 ± 58.9 cm·s^{-1} (BL/s: 7.39 ± 2.74, $N = 77$) before capture.

No significant effects of time (before or after the angling experiments) or predator type were detected using LMMs (lmer with individual as a random factor) in any of the three performance measures (Fig. 5 and Table 4).

Performance comparison of pike in predation and angling trials

Differences in the three performance parameters were tested using LMM with predator type (two levels: fast and slow responders) and trial type (two levels: predation and angling experiment) as explanatory variables and individual as a random factor. This analysis showed a significant effect of trial type on distance at orientation (LMM overall model significance: 187 observations, $r^2_{adj.} = 0.11$; trial type $F_{[1,183]} = 16.0$, $p < 0.0001$); pike oriented themselves from a greater distance in the predation trials compared with the angling trials. This difference in orientation distance was not affected by predator type ($F_{[1,183]} = 2.2$, $p > 0.10$; Table 5). No significant effects of trial and/or predator type were found for distance at attack (LMM overall model significance; 133 observations, $r^2_{adj.} = 0.02$, all $p > 0.10$) and maximum speed during the attack (LMM overall model significance; 133 observations, $r^2_{adj.} = -0.01$, all $p > 0.10$).

Discussion

Northern pike showed bimodal distribution in the latency to attack prey under altered environmental conditions as a stressor. The classification of fast responding (proactive) and slow responding (reactive) pike was consistent over three repeated behavioral trials performed at a 15-day period and showed low misclassification values of between 2% and 23%. Due to this high level of consistency over time, the variation in foraging latency between individuals was interpreted as variation in their predator type (sensu Koolhaas et al. 1999; Dingemanse and Réale 2005). Fast responders showed higher acceptance of bait than slow responders did in simulated angling trials, providing support for the hypothesis that angling may affect local fish populations through inflicting selective mortality.

Predator types in pike

Analysis of individual variance in the latency to attack a prey during the presence of a stressor (light) resulted in two distinct clusters: pike that attacked the prey instantly (within approx. 2 min) vs. pike that attacked after a long latency (after 10 min). This bimodality in pike predator behavior was supported by the result that within individual repeatability (R), attack latencies in the behavioral trials decreased from 0.51 when calculated over all individuals to <0.01 when calculated separately for each cluster. This value of repeatability is common for behavioral traits (Bell et al. 2009). The finding of distinct behavioral strategies is in line with previous results of two field studies on pike that found multimodal distributions in activity and habitat use as well as in timing of migration and proposed these to be a result of natural selection (Kobler et al. 2009; Tibblin et al. 2016). Additionally, Laskowski et al. (2016) found consistent variation in the activity level, with more active, interpreted as bolder, pike being exposed to a higher risk of cannibalism or piscivory than less active pike. Furthermore, repeatable individual foraging behavior under risk as an indicator for boldness was shown for juvenile stages of pike (Nyqvist et al. 2012), and a connection between behavioral types in predator behavior of pike and predator avoidance behavior of prey was found (McGhee et al. 2013). Moreover, individual repeatable behavioral responses in maze tests and novel object tests have been found even in pike larvae (Pasquet et al. 2016). Together, these publications plead for strong consistency between different measurements that include variation in boldness in pike behavior. As boldness has been shown to be heritable in fish (Kortet et al. 2014) and fishing vulnerability is subject to selection (Philipp et al. 2009), it is important to further monitor whether selective angling could result in decreased variability in the expression of such predator traits in pike.

In contrast to previous studies showing consistent phenotypic variation in pike in natural conditions (Kobler et al. 2009; Monk et al. 2021), this study measured latency to forage under temporary increased light conditions while all other factors were kept equal between measurements. An increase in light intensity acts as a potential stressor to the pike, as it has been previously shown, to strongly reduce the activity in pike (Laskowski et al. 2016) and, furthermore, it has been shown that abrupt changes in light intensity elicit stress responses in fish (Ryu et al. 2020). Pioneering studies on personality-like traits in rats and birds have shown that after exposure to a stressor, reactive animals become strongly inhibited, whereas proactive animals are more likely to respond to stimuli in a routine-like manner (Van Oortmerssen et al. 1990; Verbeek et al. 1996). Additionally, behavioral responses to unfamiliar environments have been shown to be different in fish that were selected for low or high cortisol responses (Schjolden et al. 2005). The current study showed that fast-responding, i.e., proactive, pike did not change their predation response over time, whereas slow-responding, i.e., reactive pike, showed a significant reduction of latencies from the first to the third behavioral trial. These fast vs. slow predator types in pike are thus characterized by variation in behavior patterns that seem similar to those described for proactive vs. reactive coping styles (Koolhaas et al. 1999; Bensky et al. 2017), with the former being more routine-like and the latter showing higher plasticity in their response to environmental change. Pike used in the current study were reared from eggs of parent animals with no angling pressure and selected at random from the reared cohort to prevent any pre-existing bias in behavioral strategies either originating from the method of capture (electrofishing, angling,

Fig. 5. Performance parameters (mean ± SD) of fast- and slow-responding pike during predation trials with live brown trout as prey before and after the angling experiments. (*a*) Distance of the pike during orientation toward the trout ($N = 39$); (*b*) distance of the pike at the start of the final acceleration before the attack ($N = 35$); and (*c*) maximum speed (mean of three highest values) of the pike during an attack ($N = 35$).

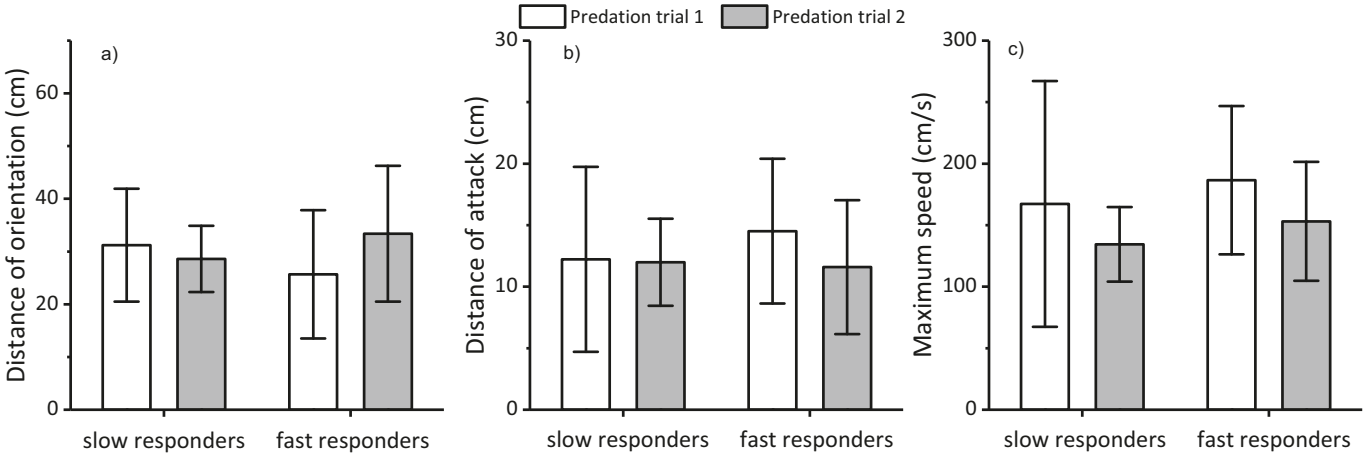


Table 4. Results of linear mixed models with predator type (fast and slow) and time (before and after the angling experiments) as explanatory variables and individual as a random factor on the performance parameters during the predation trials recording the hunting behavior under habituated conditions of pike.

Variable	*N*	Predator type (fast and slow)	Time (trials 1 and 2)	Predator type × time
Distance at orientation (cm)	81	$F_{[1,41.0]} = 0.25,\ p > 0.05$	$F_{[1,41.0]} = 0.78,\ p > 0.05$	$F_{[1,41.0]} = 3.53,\ p > 0.05$
Distance at attack (cm)	77	$F_{[1,44.7]} = 1.21,\ p > 0.05$	$F_{[1,44.7]} = 0.19,\ p > 0.05$	$F_{[1,44.7]} = 2.58,\ p > 0.05$
Maximum speed ($cm \cdot s^{-1}$)	77	$F_{[1,44.7]} = 1.41,\ p > 0.05$	$F_{[1,44.7]} = 3.14,\ p > 0.05$	$F_{[1,44.7]} = 0.24,\ p > 0.05$

Table 5. Results of the linear mixed model showing the influence of explanatory variables on the distance at orientation of the pike in angling and predation trials (187 observations).

Response distance orientation (cm)			
Variables	df	*F* ratio	Prob > *F*
Trial type (angling vs. predation on natural prey)	1.183	16.005	*<0.0001*
Predator type	1.183	2.2241	0.136
Predator type × trial type (angling vs. predation on natural prey)	1.183	0.463	0.497

Note: Individuals were added as random factors to the model.

or traps) or due to previous lure exposure (Laskowski et al. 2016; Røste 2020). In this unbiased sample, proactive vs. reactive predator types in pike were present at a ratio of two to one.

Angling selectivity

Proactive predator-type individuals were more likely than reactive predator-type individuals to attack a fishing bait, regardless of bait type, thus rendering them potentially more sensitive to fishing mortality. This effect of angling is in agreement with a field study in pike showing that angling can affect the composition of behavioral phenotypes by selectively targeting individuals with high activity (Monk et al. 2021), a trait that is correlated with boldness (Sneddon 2003; Bell 2005; Harcourt et al. 2009). Although this result may not be generalized for other species, as, e.g., no relation between catchability and boldness was found in perch (*Perca fluviatilis*) (Härkönen et al. 2016) and in muskellunge (Bieber et al. 2023), these studies provide positive support for a "selective-angling hypothesis" for pike. As pike are apex predators, which likely have a structuring effect on their prey fish populations (Craig 2008) and might have indirect effects via trophic cascades on the whole ecosystem (Drenner and Hambright 2002; Ripple et al. 2016), studying consequences of selective removal of behavioral phenotypes of pike is an important avenue for research. Here it should be noted that in the wild, pike are constantly exposed to biotic and abiotic variability, and in this broader context of environmental stressors, proactive or reactive predator types might also forage differently in their natural habitat. The current findings therefore support the call of Nannini et al. (2011) and Bieber et al. (2023) to investigate the consequences of fishing methods that remove

predators with specific traits on the management of natural fish populations and how this might affect the quality of the recreational fishery.

One potential measure to balance the effects of selective fishing would be the application of alternative capturing methods that target one or the other predator type of pike. Such an alternative angling effect has been demonstrated in largemouth bass (Wilson et al. 2015) and brown trout (Vainikka et al. 2021). In the current study using simulated angling, three bait types were tested, including a soft plastic natural-colored lure, a soft plastic bright-colored lure, and a natural dead baitfish. Predator types did not respond differently to any of these bait types. One important difference between the current study and that of Wilson et al. (2015) was that the latter not only tested different lure types but also deployed different angling methods. Shy bass snapped more often at the natural-colored, soft rubber lure, which was offered very slowly, while bold bass also struck at the artificial lure in bright colors, which was equipped with an internal rattle and was presented very quickly. Therefore, investigating the vulnerability of proactive and reactive predator types of pike to angling using a wider range of baits or angling techniques than used in the current study remains an interesting avenue for future experiments.

Bait handling and bait avoidance

Although none of the bait types used in the angling experiment seemed to be as stimulating as natural prey, there were clear differences in the way bait types were handled by pike following a successful strike. The dead baitfish was statistically more likely to be kept in the mouth compared to soft plastic baits, which were spat out after capture. This is likely explained by the fact that the natural bait was much the same as the natural living prey that the pike were accustomed to feeding on, with the difference that the bait was freshly defrosted. Thus, dead bait exhibited a smell and texture similar to familiar prey. Hence, fishing with natural bait results in greater swallowing depth, which during angling with hooks poses a greater risk of injury to the gills and esophagus (Arlinghaus et al. 2008). When a pike swallows the bait deep, there might also be a greater likelihood that the fish will hook itself without any action on the part of the angler. In addition, if the bait has a higher retention time in the mouth of the pike, the angler may have more time to recognize the bite and set the hook. Consequently, the natural bait may contribute more to fishing mortality in intensively fished waters, especially where catch-and-release angling is practiced (Dubois et al. 1994).

One consequence of the repeated handling of bait in the angling experiment was that the probability of an attack decreased with each new encounter with any bait. This learned "bait avoidance" behavior was equally apparent in both predator types. Learned bait avoidance has been proposed to explain the decline in catch rates when angling for northern pike using artificial baits (Kuparinen et al. 2010). Furthermore, this learning depends on bait type, as the foraging response to metal spoons decreased faster than that to soft plastic lures (Arlinghaus et al. 2017*a*, 2017*b*). Moreover, a field study using live bait fish did not show such a decline in pike catch rates, whereas that study also found a sharp decrease in the tendency of pike to attack artificial lures over several days of angling (Beukema 1970). Pike might not be able to develop avoidance learning from live bait as these emit stimuli in the form of natural swimming movements that are associated with capturing normal prey, and these are clearly distinct from mechanically animated dead fish as used in the current setup. Studies with largemouth bass indicated that fishing effort and even the similarity of a novel lure to previously experienced lures may determine if a fish avoids angling capture (Wegener et al. 2018; Louison et al. 2019). Also, in Atlantic salmon, an avoidance of familiar bait types after capture and release was recorded (Lennox et al. 2016). With all baits in the experiment having a similar silhouette and being moved in a similar pattern, learning could explain the bait avoidance of the pike over time. Clearly, pike are able to separate behaviorally divergent (dead) bait from their natural live prey, and to associate them with the angling event and learn to avoid such bait in subsequent encounters.

Performance, predator type, and predation

As individuals were found to clearly differ in attack latency under the application of a temporal stressor, the question was raised whether these individuals would also respond differently in their predator performance under habituated conditions. None of the performance variables measured here, i.e., distance at orientation of the pike to the bait, distance at commencement of attack, and maximum velocity during final acceleration, suggested that this is the case. Furthermore, pike in both groups were similarly sized, and no differences in measured speed were observed.

An early kinematic study was carried out on nearly twice as large pike as in the current study. It used accelerometers as a method (Harper and Blake 1991) and reported attack speeds that were a factor two higher than in the current study, which is expected as swimming performance scales positively with body size in pike (Cano-Barbacil et al. 2020). In a recent study, kinematic metrics (distance attack and maximum speed) were published for the hunting of pike during predation on schools of fish that were similar in size to the pike in the current study (Jolles et al. 2021). They reported slightly lower maximum speeds (122.7 ± 40.1 cm·s^{-1} vs. 158.9 ± 42.4 cm·s^{-1} and 164.9 ± 58.9 cm·s^{-1}, t-test $p < 0.05$), which may be explained by the fact that these pike were targeting a school of prey vs. single prey in the current study. Pike that target prey in a school tend to launch an attack from a closer distance than those targeting single trout. However, a pike launching an initial attack on a complex moving school may subsequently focus in on a single escaping individual. Measuring the distance from predator to the centroid of a school at the start of an attack results in similar values for predator and prey to those seen in the current study (11.7 ± 4.4 cm and 12.7 ± 5.6 cm vs. 11.5 ± 6.0 cm). Together, this indicates that motor control of predation, in which the posterior placement of the dorsal and anal fins and the long body shape of pike play an important role (Frith and Blake 1991), follows a tightly controlled program for closing in on

the target and which often ends with successful swallowing of prey. The motor pattern of predation thereby closely follows the description of a modal action pattern (Barlow 1977; Lankheet et al. 2016). Differences between proactive and reactive predator types in pike are therefore likely to influence predation-releasing mechanisms rather than motor control of predation.

The results imply that fast-responding/proactive pike are not necessarily energetically more active than slow-responding/reactive pike, which aligns with a previous study in which it was concluded that pike personality was not the result of metabolic differences as suggested by the "pace-of-life hypothesis" (Laskowski et al. 2016). In short, this hypothesis postulates that variations in behaviors are caused by variations in slower changing state variables such as metabolic rate or body condition, which in turn are consistently related to life history traits such as growth rate, reproductive effort, and mortality rate. From this hypothesis, it can be inferred that animals with low physical condition and animals with a high metabolic rate would both undertake riskier behavior to compensate for low energy reserves or meet their energy demands (Biro and Stamps 2008, 2010; Závorka et al. 2015). However, neither metabolic rate nor condition was related to personality-like traits of pike in the field (Laskowski et al. 2016). In addition, in the current study, no difference was found between behavioral strategy and size (all randomly selected fish had similar ages) or condition. The differences found between fast and slow predator types therefore might constitute alternative behavioral strategies that might offer selective advantages for predation through frequency dependency rather than through life-history-related mechanisms (Abrams and Matsuda 1993; McCauley et al. 1993).

The performance of pike targeting natural prey under habituated conditions, such as the live brown trout offered in the current predation trials, did not change from the start to the end of the experiment, even though the pike developed bait avoidance in between predation trials. This suggests that pike can quickly and effectively learn to distinguish between real prey and bait, where, as discussed before, the natural prey movement is likely to be the key releaser for an attack and the characteristic that most clearly distinguishes natural prey from dead bait and plastic lures. An ability to differentiate between these stimuli is clearly indicated in the significantly earlier orientation of pike toward live prey compared to baits (measured as a larger orientation distance). This indicates that adverse experience with bait did not affect predation behavior under the standardized and habituated conditions, which is relevant from the perspective of evaluating the potential effects of angling on pike. It must be noted, however, that the current study did not include hooking and handling of the pike that would occur during a failed angling attempt or in catch and release. Catch and release has been found to have effects on growth and habitat use as well as short-term effects on foraging behavior in pike (Klefoth et al. 2011; Stålhammar et al. 2012), but does not appear to have a lasting effect on pike behavior (Klefoth et al. 2008; Baktoft et al. 2013; Flink et al. 2021). The current study supports the idea that pike are capable of learning from such events and that such avoidance learning effects occur across predator types.

Conclusion

The existence of fish with different behavioral strategies that differ in vulnerability to fishing methods is of interest to both behavioral scientists and fisheries managers. The current study indicates that even without bait selectivity, a popular angling method in a controlled environment can selectively target fish based on their predator type (fast responders, i.e., proactive vs. slow responders, i.e., reactive). These results add to earlier reports that raise concerns about fishery-induced selection (see Monk et al. 2021) (in this case, "selective-angling") on behavioral diversity in predator behavior of northern pike. Pike of the reactive predator type may be easily dissuaded from their natural hunting behavior by stressors in general and are thereby less likely to be captured by angling. From a management perspective, more reactive individuals in the population due to harvest in combination with possible post-release mortality and the additional learned bait avoidance in released individuals could lead to incorrect estimations of the population of predators in the ecosystem if this estimation is based on angling data. It could also negatively impact catch rates and the quality of the fishery (Conover and Munch 2002; Alós et al. 2015; Andersen et al. 2018; Monk et al. 2021). In order to ensure the preservation of the different phenotypes, the use of best fishing practices is preferable, as avoiding angling-induced mortality in pike can also prevent evolutionary effects (Matsumura et al. 2011). These practices include the use of appropriately sized gear to minimize time spent fighting the fish and reduce potential disturbance (Brownscombe et al. 2017). Furthermore, care should be taken to avoid catching animals at high temperatures (Gingerich et al. 2007) and to minimize air exposure (Arlinghaus et al. 2009*a*). It could also be considered to establish protected areas, as this may prevent incidental angling-induced mortality and harvest and lead to the protection of sensitive phenotypes, as previously shown for other angler-preferred predators (Cooke et al. 2017). Additionally, learning effects could be potentially counteracted by reducing stress on the animals during capture through the best possible capture practices just described and giving them ample time to recover (Kuparinen et al. 2010; Koeck et al. 2020). Further research comparing different angling methods and bait types is important to determine the extent to which such anthropogenic selection in fisheries can alter the phenotypic and genetic composition of natural populations over time and to gain a better understanding of how to develop more sustainable management of recreational fisheries. Though different circumstances may exist in other populations and species, the results suggest that this selective-fishing effect should be taken into account in future evaluations of recreational fisheries.

Acknowledgements

We thank the "Angelverein Illmensee e.V." and Friedhelm Glönkler for their kind donation of pike larvae. Special thanks to Andreas Revermann for his help with capturing adult pike in the "Ruschweiler See". Furthermore, very special thanks to Philipp Tölle and the team at FFS Langenargen

for the help of rearing the pike and building the experimental setup. Special thanks to Amy-Jane Beer and two anonymous reviewers for improving the manuscript.

Article information

History dates

Received: 9 January 2023
Accepted: 11 August 2023
Version of record online: 17 October 2023

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Data availability

Data used to generate tables, figures, and plots as well as R and Arduino code used during the study and for analyses are made available from Figshare (https://doi.org/10.6084/m9.figshare.24146418). All code used published packages.

Author information

Author ORCIDs

Jorrit Lucas https://orcid.org/0000-0001-5374-495X
Albert Ros https://orcid.org/0000-0003-3241-9722
Juergen Geist https://orcid.org/0000-0001-7698-3443
Alexander Brinker https://orcid.org/0000-0002-2433-5652

Author contributions

Conceptualization: JL, AR, JG, AB
Data curation: JL
Formal analysis: JL, AB
Investigation: JL
Methodology: JL, AR, JG, AB
Project administration: AB
Resources: JL
Supervision: JG, AB
Validation: JL
Visualization: JL
Writing – original draft: JL
Writing – review & editing: AR, JG, AB

Competing interests

The authors declare there are no competing interests.

Funding information

The authors declare no specific funding for this work.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2023-0004.

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