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Hook Avoidance Induced by Private and Social Learning in Common Carp

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Abstract

It is essential for fish to respond appropriately when faced with a threatening situation. Accordingly, fish are able to reduce predation risk through learning. In addition to privately learned experiences, fish can acquire social information about a threat by observing the response of conspecifics and use such public information to adapt future behavior through learning. It is unclear if social learning can also influence the behavioral response of fish when faced with human-induced threats in the form of angling. Using an experimental approach in the laboratory, we examined the influence of private (i.e., direct experience of hooking) and social information on angling vulnerability in Common Carp *Cyprinus carpio*—a species regularly exposed to catch-and-release angling. Compared with control groups, individuals with direct or social experience of catch-and-release angling expressed significantly elevated hook avoidance behavior during a short-term vulnerability assessment hours after a catch-and-release experience. In the medium-term vulnerability assessment, conducted within days after the threat event, fish with direct hooking experience continued to exhibit decreased angling vulnerability, whereas the social experience of catch and release did not consistently reduce angling vulnerability compared with controls. Yet, in a subsequent trial within days after the threat exposure, we found that fish with direct hooking experience and fish with only social hooking experience were both more cautious towards bait (corn) in the presence of a sham rig (i.e., a hookless rig with bait) than when only exposed to bait without a rig. Collectively, these results indicated that the combined influence of direct and social experience of catch-and-release angling induced a hook avoidance behavior in Common Carp. The extent to which the phenomenon of social hook avoidance learning exists in other recreationally targeted fish species and in the wild deserves further attention because of the potential to affect catch rates and population-level catchability.

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Animal learning refers to a change in behavior with experience (Dill 1983; Kieffer and Colgan 1992), which is of pivotal importance to understanding sexual selection, foraging decisions, and threat avoidance behavior (Brown et al. 2003). Fish have the ability to learn from private experiences (i.e., private learning), but also from social information (i.e., social learning; Kieffer and Colgan 1992; Heyes 1994; Brown and Laland 2003), and change behavior in various contexts, such as migration (Helfman and Schultz 1984), resource acquisition (Laland and Williams 1997; Harcourt et al. 2010), and risk assessment (Suboski et al. 1990; Brown and Laland 2003; Kelley and Magurran 2003; Griffin 2004). Specifically in risky situations, the capacity for social learning presents a strong advantage over private learning as naïve individuals can acquire information from the observation of experienced heterospecifics and conspecifics in threatening situations without exposing themselves directly to the risk of predation (Mathis et al. 1996; Griffin 2004).

One applied field where fish behavior and learning has gained recent attention is in the context of recreational catch-and-release fishing. Catch and release can be mandatory for anglers to comply with harvest regulations or be conducted voluntarily due to personal ethic (Arlinghaus et al. 2007). For instance, catch-and-release rates in some recreational fisheries in North America and Europe have increased during the last decades, such as in specialized fisheries for Largemouth Bass *Micropterus salmoides* (Myers et al. 2008), Muskellunge *Esox masquinongy* (Fayram 2003), Northern Pike *Esox lucius* (Margenau et al. 2003), and Common Carp *Cyprinus carpio* (Arlinghaus 2007). Catch and release has sublethal effects on fish (e.g., inducing hooking-related injuries and physiological stress responses; Pankhurst and Dedual 1994; Meka and McCormick 2005), which can lead to behavioral changes in released fish, such as decreased activity (Schreer et al. 2005; Halttunen et al. 2010; Klefoth et al. 2011) and altered feeding (Stålhammar et al. 2012). The experience of being captured and released can also induce hook avoidance learning, which has been documented in as diverse species as Common Carp (Beukema 1970a; Raat 1985; Klefoth et al. 2013), Northern Pike (Beukema 1970b; Arlinghaus et al. 2017a, 2017b), Largemouth Bass (Anderson and Heman 1969; Wegener et al. 2018; Louison et al. 2019b), and Rainbow Trout *Oncorhynchus mykiss* (Askey et al. 2006; Lovén Wallerius et al. 2019; Koeck et al. 2020). Hook avoidance learning decreases overall angling vulnerability and can penalize future catch rates (Beukema 1970a, 1970b; van Poorten and Post 2005; Klefoth et al. 2013; Monk and Arlinghaus 2017). Reduced catch rates not only affect angler satisfaction negatively (Arlinghaus et al. 2014; Beardmore et al. 2015) but may also negatively affect stock assessments that rely on catch rates as indicators of stock abundance (Alós et al. 2019).

Mechanistically, hooked and released fish learn from private hooking experiences (Beukema 1970a; Raat 1985; Louison et al. 2019b; Lovén Wallerius et al. 2019). In addition, it has been suggested that fish may also rely on socially transmitted cues that indicate threat, such as behavioral cues or the release of alarm pheromones (also called Schreckstoff) through injury of the epidermis (Pitcher 1993), to avoid future capture by angling (Beukema 1970a; Klefoth et al. 2013; Lovén Wallerius et al. 2019; Koeck et al. 2020) or other fishing gear (Brown and Warburton 1999; Brown and Laland 2002). Compared to the effects of private learning (i.e., direct effects of hooking), it remains largely unexplored to what extent social learning (i.e., the experience of watching conspecifics being caught) can affect individual vulnerability to capture in the future. Only a few studies have explicitly examined the role of social learning in hook avoidance behavior of fish. Studies by Wegener et al. (2018), Lovén Wallerius et al. (2019), and Louison et al. (2019b) suggest that social learning does not affect angling vulnerability of Largemouth Bass and Rainbow Trout, but Lovén Wallerius et al. (2019) showed that in Rainbow Trout the social experience of catch-and-release angling induced a stress response compared with naïve individuals, suggesting that Rainbow Trout realized the threat. Moreover, in both Wegener et al. (2018) and Louison et al. (2019b) catch rates declined over time in experimental angling trials, with only a fraction of the stock being captured, either implying that there is a large pool of invulnerable fish or that some form of social learning took place to reduce reactivity to the gear. Indeed, Klefoth et al. (2013) showed that an entire group of Common Carp was developing hook avoidance rapidly after just a few days of angling, despite only a fraction of the stock being hooked. Contrasting results on whether social learning affects hook avoidance in fish may be caused by methodological issues or be explained by species-specific differences in cognitive abilities (Coble et al. 1985), sociality (Bisazza et al. 2000), or the social learning mechanism that is tested (Brown and Laland 2003; Rendell et al. 2011).

Common Carp is an important species for recreational fishing, particularly in Europe, and there are specialized fisheries targeting large trophy fish through total catch and release (Arlinghaus 2007). Earlier angling studies on Common Carp suggest that a single hooking event can lead to hook avoidance even after a year (Beukema 1970a), and although not experimentally shown through a controlled design, previous work in group-held Common Carp populations have suggested that social hook avoidance learning might be at play in this species (Klefoth et al. 2013; Monk and Arlinghaus 2017). Examining the relationship between social learning and acquired hook avoidance in Common Carp—an omnivorous and highly social fish species (Huntingford et al. 2010) with better

developed learning abilities relative to less social predatory fish (Coble et al. 1985)—will shed further light on the question of whether social hook avoidance learning is possible or not in teleost fish.

We experimentally examined the relative importance of social learning compared with private learning in Common Carp and their influence on hook avoidance over the course of several days in laboratory trials. We predicted that (1) direct exposure to catch and release (i.e., private learning of hooking) will increase future hook avoidance in Common Carp compared with naive control fish, (2) social exposure to catch and release will also increase hook avoidance compared with naive fish but not to the same extent as with direct experience, and (3) hook avoidance generated by direct and social experience will be most pronounced immediately after capture and persist over time to a greater extent in fish exposed to a direct hooking experience than in those with a social hooking experience.

METHODS

Overview

We conducted an angling experiment over three consecutive rounds to assess short (2 h) and medium-term (5–7 d) hook avoidance of Common Carp in response to previous experience of angling following four different treatments or controls (Figure 1). The angling treatments consisted of the following:

1. Direct or social exposure: two fish were introduced to the same aquarium and exposed to one angling rig (description of angling rig below). Because no fish had experienced angling before, assignment to direct or social exposure happened during the angling exposure (Figure 1A), after the hooking of one of the two individuals, rendering the unhooked fish a social exposure and the hooked fish a direct exposure ($N=34$ direct and $N=33$ social; one social exposure individual died during the experiment).

2. Control single: introduction of one fish in an aquarium and exposure to a hookless, nonthreatening sham rig with a bait ($N=24$).

3. Control pairs: to account for the changing social context in the subsequent medium-term vulnerability assessment, where the individuals from all treatments were retested individually (Figure 1B to Figure 1C), an additional control treatment was included. Two fish were introduced to the same aquaria and exposed to a hookless nonthreatening sham rig with a bait ($N=24$).

Following the angling exposure (Figure 1A), all fish were kept and retested in the same aquaria (without changing group composition) with a hookless sham rig 2 h

after the first exposure to the angling rig (Figure 1B). After the 2-h short-term vulnerability assessment, fish were removed from the aquaria and stocked in four different holding tanks. A medium-term vulnerability assessment was conducted 5 to 7 d after initial angling exposure. Here, all fish were individually retested in the aquaria with a hookless sham rig to assess whether hook avoidance would be sustained for up to a week following the first angling exposure (Figure 1C). To test the avoidance behavior towards corn alone or corn in the presence of a sham rig, 2 h after the medium-term vulnerability assessment all individuals were randomly assigned into two additional treatments, one where corn was introduced (corn first) or one where corn was introduced alongside a corn-baited sham rig (sham first) (Figure 1D). For all angling and sham-rig treatments, latency to ingest a corn-baited rig (i.e., time until individual ingested the corn) was used to calculate the hook avoidance behavior of the fish. Previous work has shown that sweet corn is a suitable bait that is readily ingested by Common Carp in laboratory settings (Klefoth et al. 2013).

Tagging, Fish, and Holding

Prior to the start of the experiment, 120 juvenile Common Carp hatched and raised in earthen ponds were stocked for 10 d in groups of 40 individuals in recirculating holding tanks ($1 \times 1 \times 0.7$ m) in the laboratory supplied with oxygenated water at a constant temperature of $17 \pm 0.5^\circ\text{C}$. Fish were fed on a daily basis with a mix of commercial pellets and sweet corn cut in three pieces. After an acclimation period of 6 d, fish were anaesthetized with a 9:1 ethanol to clove oil solution (1 mL/L) in well aerated water at $17 \pm 0.5^\circ\text{C}$, measured for total length (mean \pm SD = 14.9 ± 1.3 cm) to the nearest 1 mm and weighed to the nearest 0.1 g (mean \pm SD = 58.4 ± 18.4 g). Following total length and mass measurements, the fish were tagged with a passive integrated transponder (11-mm PIT tag; Oregon RFID, Portland) in the abdominal cavity. After PIT tagging, all fish were returned to the holding tanks and allowed to recover for a period of at least 4 d.

Experimental Design

The angling exposure was conducted in three recirculating systems placed side by side in the same climate-controlled room. Each recirculating system contained eight glass aquaria ($50 \times 30 \times 30$ cm). Each aquarium included a stone (approximately 8×8 cm) and a plastic plant in the back end for cover and was supplied with oxygen. Each angling round started with the introduction of 40 individuals haphazardly netted from the same holding tank and randomly distributed in the glass aquaria. Of the 40 individuals, 8 were assigned to control single (8 aquaria), 8 to control pairs (4 aquaria), and 24 to direct or social exposure (12 aquaria). Since no fish had experienced angling or hooking before, the direct and social exposure was

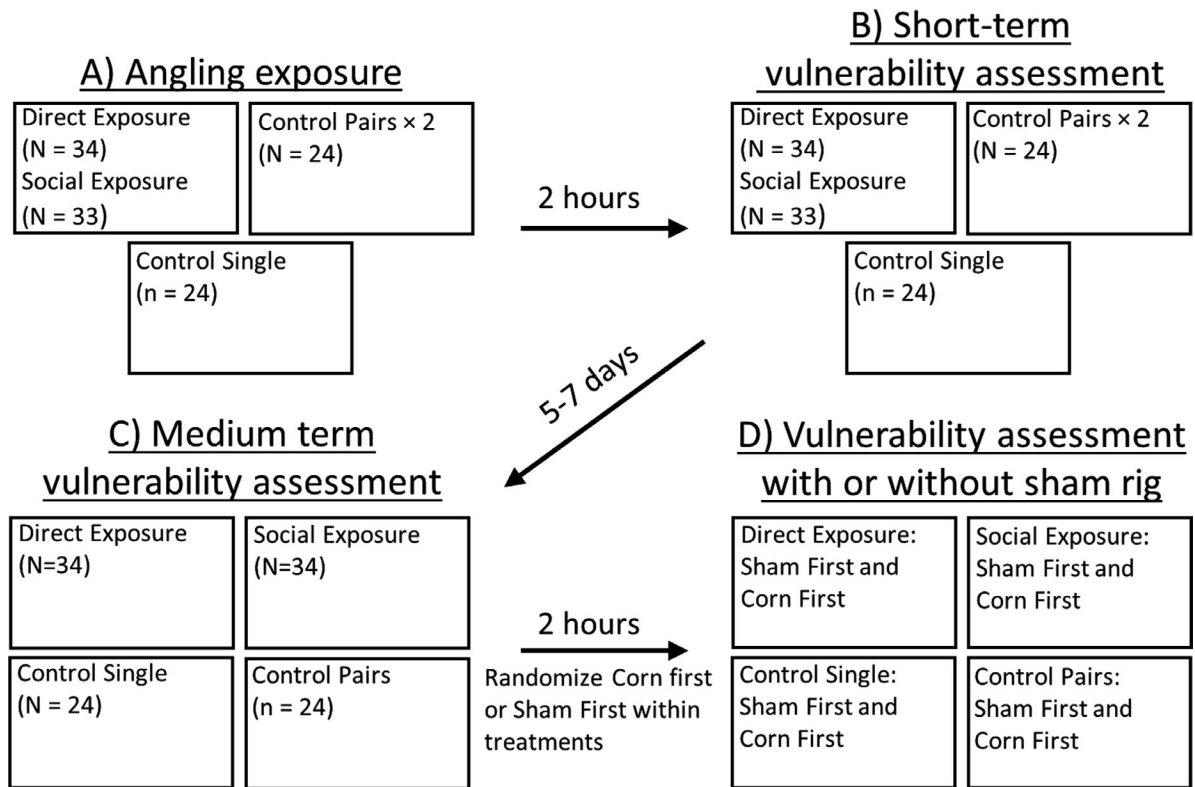


FIGURE 1. Schematic figure of the experimental setup with the different angling treatments in each aquaria in (A) angling exposure, (B) short-term vulnerability assessment, (C) medium-term vulnerability assessment, and (D) vulnerability assessment with or without sham rig. After the angling exposure and short-term vulnerability assessment, individuals originating from direct or social exposure and control pairs were individually retested in the aquaria for the subsequent medium-term vulnerability assessment and vulnerability assessment with or without sham rig. In panel D “corn first” and “sham first” refer to the assessment of corn without the presence of a sham rig and corn in the presence of a sham rig, respectively.

conducted in the same aquaria, and fish were assigned to either the direct or social exposure depending on whether an individual was hooked or not during the subsequent angling exposure. After introduction to the aquaria, fish were left to acclimate for 3 d and all aquaria were individually covered with a black curtain at the front end to minimize disturbance before any treatment. In addition, dividers were put down between the long sides of each aquaria to avoid visual contact between aquaria. To reduce the possibility of stress in the control single treatment and allow a quasisocial experience during the acclimation phase, no dividers were put down between fish in this treatment so they could have visual contact with another fish from control single as the other two treatment groups (direct or social exposure and control pairs) were initially held in pairs. Ten minutes before feeding exposure or angling or sham exposure, the recirculation system was shut off to stop further chemical communication between aquaria, dividers were put down between control single treatments, and the black curtain was removed.

One day before angling exposure, a feeding trial was conducted to test the initial affinity for corn pieces versus pellets before being exposed to the angling experience. The fish in the control single treatment was given three corn pieces and three pellets, whereas fish in the control pairs and direct and social exposure treatments were given six corn pieces and six pellets. Pellets were 4×2.5 mm, whereas the corn pieces were 5×5 mm. Feeding trials were video recorded for 10 min using webcams (Logitech C920) and the proportion of pellets or corn eaten was measured. This trial assessed the food type preferences and followed a related approach of a previous study to assess food preference in Common Carp (i.e., Klefoth et al. 2013).

Angling Exposure

Direct or social exposure.— During the angling exposure (Figure 1A), fish in the direct and social treatment were exposed to an angling rig consisting of a 15-cm braided leader (resistance 10 kg) with two lead weights (1.8 and 1.0 g) attached 5 cm from the hook (Gamakatsu, microbarbed, size 14), tied to a 1.5-m nylon line (0.25 mm, 3.85 kg).

Before the angling rig was introduced to the aquaria, a sweet corn piece was attached to the hook. When one fish had ingested the hook with corn, the observer (standing hidden to the side of the aquaria to avoid unnecessary disturbance) pulled the rig to hook the fish, rendering that individual directly exposed and the other socially exposed. To allow further social stimuli between the two fish and mimic a typical struggle experience during angling, the hooked fish was kept on the line for 30 sec. After 30 seconds, the hooked fish was netted and air exposed for 30 sec. During this time, the fish was identified and unhooked. After air exposure, the fish was released back to the same aquarium. After angling exposure in one aquarium, the black curtain was put back to reduce disturbance when the observer was moving around in the room. Control pairs and control single experienced a similarly built rig but without the hook (hereafter referred to as a “sham rig”); instead the corn piece was attached to the leader on a nylon loop. The angling and sham rig exposures lasted for 10 min and were video recorded during the whole period.

Short-term vulnerability retest.—To test short-term vulnerability towards the angling rig (Figure 1B), a sham rig with a corn piece attached was introduced 2 h after the initial angling exposure and the latency to ingest the corn was recorded (i.e., when corn was ingested for the first time). After the retest, all fish were stocked in the same holding tank (for dimensions see above) and allowed to rest until the medium-term vulnerability assessment (see below), and the water in the three recirculation systems was changed. During this time fish were only fed with pellets.

Medium-term vulnerability retest.—To test the duration of possible learning effects related to the angling exposure, the same fish were haphazardly netted and introduced randomly in the glass aquaria to allow acclimation 2 d before the experiment. As the number of aquaria was limited, all fish could not be introduced at the same time. Thus, fish were retested either 5 d or 7 d after the initial exposure to the angling or sham rig to simulate a scenario where angling is focused around weekends. After introduction, dividers between the aquaria were arranged so two individuals could have visual contact during the acclimation period. On the day after introduction, fish were fed with three pellets. The medium-term vulnerability retest was performed in the same way as the short-term vulnerability assessment but 5 to 7 d after the initial exposure to the hook (Figure 1C).

Vulnerability assessment with or without sham rig.—To test the avoidance behavior towards the corn piece itself and differentiate it from avoidance behavior towards corn in the presence of a corn-baited sham rig, 2 h after the medium-term vulnerability assessment, the same fish were randomly assigned into two additional treatments—one where food (one pellet, one corn) was introduced (corn

first) or one where a corn-baited sham rig was introduced alongside one pellet and one free corn piece (sham first) (Figure 1D). Each treatment was video recorded for 7.5 min and latency to ingest corn with or without the presence of the sham rig was noted.

Data Handling

All data were assessed to ensure that they did not violate the assumptions of the chosen statistical models. Prefeeding data were analyzed with two generalized linear models (“glm” function in the stats package for R) with binomial proportion distribution, one for proportion of corn eaten and one for proportion of pellets eaten. As paired treatments (direct and social exposure and control pairs) were given six corn and six pellets, trials were set to six for each feed type. In control single, trials were set to three for each feed. For both models, the proportion of corn or proportion of pellets was used as a response variable and fish mass was included as explanatory variable. A Cox proportional hazard regression (“coxph” function, “survival” package in R) was estimated to analyze associations between treatments and time-to-event occurrence (i.e., to what degree the different treatments affected the latency to ingest the corn). Additionally, to explore relationships between vulnerability to angling and individual differences in mass, mass was included as a time-independent covariate in the Cox proportional hazard regression. The model accounted for only one event per individual (i.e., the response variable was time to ingest corn for the first time). All exposures assessing vulnerability to angling (i.e., hooking and subsequent retests with the sham rig) had similarly built models. For the initial angling exposure model, individuals in the paired control treatment were omitted from the model when the corn was eaten in ≤ 10 sec by the other individual ($n = 6$), as these had no chance to take the corn. In addition, all social individuals were removed from the initial angling model as these individuals only got the stimuli from the hooking. The model analyzing short-term angling vulnerability also omitted individuals in the paired control treatment when the corn was eaten in ≤ 10 sec by the other individual ($n = 6$). In the medium-term vulnerability assessment model, 5 and 7 d were pooled to maintain sample sizes and avoid loss of power in the Cox proportional hazard regression. In the vulnerability assessment with or without sham rig, latency to ingest the corn was used as the response variable to test the difference between treatment groups. Angling vulnerability was calculated using the model output $[\exp(\text{coef}) - 1] \times 100$, following Austin (2017), where an initial value of $\exp(\text{coef}) < 1$ indicates a decrease in vulnerability, and an initial value of $\exp(\text{coef}) > 1$ indicates an increase in vulnerability. All statistical analyses were conducted using R, version 3.5.0 (R Core Team 2018).

RESULTS

Prefeeding

Fish assigned to the direct exposure ate significantly more corn than fish assigned to the social treatment and fish in the control pairs treatment but not more than individuals in the control single treatment (Table 1; Figure 2A). Yet, there was no difference in the proportion of corn eaten when analyzing the direct and social individuals as a group compared to controls ($Z=0.0465$, $P=0.642$). When comparing the proportion of pellets eaten, larger fish ate more pellets and fish in the control single treatment ate more pellets than all other treatments, whereas no significant difference was found between fish from the direct and social treatments (Table 1; Figure 2B).

Angling Exposure and Short-Term Vulnerability Retest

No significant differences in latency to ingest the angling rig were found between the treatments during the initial angling exposure (Table 2; Figure 3), but larger individuals were faster to approach the angling rig during the initial angling treatment (Table 2). In the short-term vulnerability retest 2 h after the hooking exposure, direct exposure individuals had a significantly reduced vulnerability to angling by 56.9% compared with control pairs and by 60.2% compared with control single fish (Table 3; Figure 4). Fish in the social exposure also had a significantly reduced vulnerability to angling by 54.4% compared with control pairs and by 56.6% compared with control single fish (Table 3; Figure 4). The reduced vulnerability to angling was identical in direct and social fish,

TABLE 1. Results of the generalized linear model analyzing the binomial proportion of the number of corn eaten between the treatments (deviance residuals: minimum = -3.2086, 1Q = -1.9741, median = -0.2019, 3Q = 1.4264, maximum = 3.9135) and the number of pellets eaten between the treatments (deviance residuals: minimum = -3.048, 1Q = -1.783, median = -0.025, 3Q = 1.219, maximum = 4.188). Individuals from the direct exposure were used as the base line level of the corresponding variables. Asterisks indicate significant differences ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$).

Coefficients	Estimate	SE	Z-value	P-value
Corn				
Intercept	-0.087	0.299	-0.291	0.770
Mass	0.004	0.004	0.849	0.395
Social exposure	-1.084	0.212	-5.107	<0.001***
Control pairs	-0.603	0.221	-2.718	<0.01**
Control single	0.799	0.299	2.673	<0.01**
Pellets				
Intercept	-2.414	0.332	-7.257	<0.001***
Mass	0.026	0.005	5.225	<0.001***
Social exposure	0.363	0.217	1.669	0.095
Control pairs	0.553	0.234	2.359	<0.05*
Control single	1.418	0.296	4.775	<0.001***

but note that the short-term fish were tested in groups and not alone. Again, larger fish were overall faster to ingest the sham rig during the short-term vulnerability retest (Table 3).

Medium-Term Vulnerability Retest

During the medium-term vulnerability assessment, fish from the direct exposure remained significantly slower to ingest the sham rig and thus had a reduced vulnerability to angling by 62.5% compared with fish in the control pairs treatment (Table 4; Figure 5) and by 73.7% compared with fish in the control single treatment ($Z=-4.381$; $P < 0.001$). In addition, fish in the direct exposure had a significantly reduced vulnerability by 49.5% compared with individuals from the social exposure ($Z=-2.428$; $P < 0.05$). No difference in vulnerability was found between fish from the social treatment and individuals originating from the control pairs treatment when all fish were tested alone and not in groups (Table 4; Figure 5). However, individuals from the social treatment maintained a significantly reduced vulnerability compared with fish originating from control single treatment ($Z=-2.27$, $P < 0.05$; 47.9% reduced vulnerability) (Figure 5).

Vulnerability Assessment with or without Sham Rig

Compared to individuals from the control pairs–corn first treatment, individuals from the social exposure–corn first treatment showed a reduced vulnerability to angling by 57.1% ($Z=-1.891$, $P=0.058$) (Table 5; Figure 6). An even stronger response was shown by individuals from the social exposure–sham first treatment, which significantly reduced their vulnerability to angling by 74.6% ($Z=-3.037$, $P < 0.01$) compared with the control pairs–corn first treatment. Both direct exposure–sham first and direct exposure–corn first had a significantly decreased vulnerability to angling compared with control pairs–corn first and reduced their vulnerability by 81.1% and 76.6%, respectively. Compared to control pairs–corn first, neither sham first nor corn first affected the vulnerability of individuals originating from the control single treatment (Table 5; Figure 6).

DISCUSSION

In agreement with previous studies (e.g., Beukema 1969; Beukema 1970a; Raat 1985; Klefoth et al. 2013), we found strong evidence that a previous direct experience (i.e., private experience and learning) of hooking reduced angling vulnerability of Common Carp compared with uncaught individuals. We also found strong experimental evidence that in the short term (i.e., within hours after catch and release) the social experience of hooking, struggle, and release induced a hook avoidance response in Common Carp that was of similar magnitude to the direct

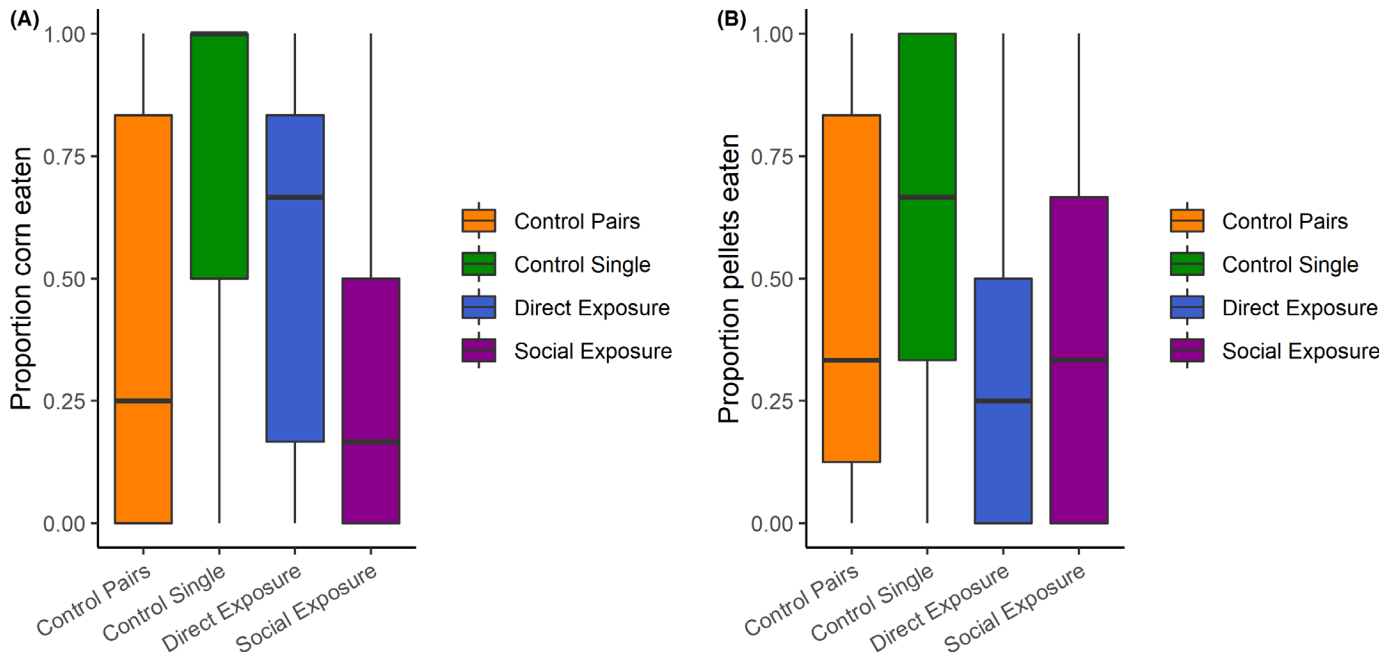


FIGURE 2. Box plots showing (A) the proportion of corn eaten in the treatments and (B) the proportion of pellets eaten in the treatments. The horizontal line in each box shows the median, the box dimensions indicate the 50% interquartile range, and the error bars represent the 95% confidence interval. [Color figure can be viewed at afsjournals.org.]

TABLE 2. Cox proportional hazard regression, estimating the effect of treatment on the time individuals remained uncaught during the initial angling exposure ($n = 109$; likelihood ratio test: 6.45, $df = 3$, $P = 0.09$). The social exposure treatment was removed as they only got the stimuli from hooking and never ingested the angling rig. The control pairs treatment was used as the reference level. The number of events = 75 and refers to the total number of caught fish. Asterisks indicate significant differences ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$).

Parameter	Estimate	Exp (coef)	SE (coef)	Z-value	P-value
Direct exposure	0.355	1.427	0.299	1.187	0.235
Control single	0.034	1.035	0.324	0.108	0.914
Mass	0.014	1.014	0.006	2.100	<0.05*

experience of hooking. When retesting angling vulnerability after 5 to 7 d using a baited sham rig, social exposure individuals retained decreased vulnerability compared with one of the control groups. By contrast, individuals with a direct hooking experience retained a decreased angling vulnerability compared with all other treatments groups, indicating that a direct hooking experience has stronger behavioral effects than just a social experience. Although these findings might suggest limited social hook avoidance learning, a follow up trial that varied the introduction of corn as bait with or without a sham rig showed that both

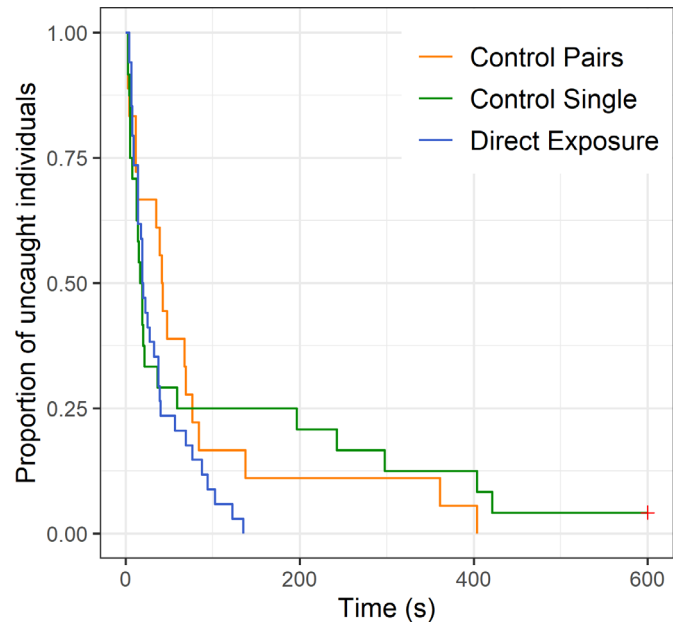


FIGURE 3. Survival curves illustrating the remaining proportions of uncaught individuals during the 600-s initial angling exposure. The time (s) to ingest a corn-baited sham rig was used as a response variable for the corresponding treatments in control pairs (orange; $N = 18$), control single (green; $N = 24$), and direct exposure (blue; $N = 34$). [Color figure can be viewed at afsjournals.org.]

direct and social exposure individuals that had previously experienced a hooking event were significantly slower to ingest the corn in the presence a of sham rig than corn

TABLE 3. Cox proportional hazard regression, estimating the effect of treatment on the time individuals remained uncaught during the short-term vulnerability retest ($n = 109$; likelihood ratio test: 15.8, $df = 4$, $P < 0.01$). The control pairs treatment was used as a reference level. The number of events = 81 and refers to the total number of caught fish. Asterisks indicate significant differences ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$).

Parameter	Estimate	Exp (coef)	SE (coef)	Z-value	P-value
Direct exposure	-0.841	0.431	0.337	-2.490	<0.05*
Social exposure	-0.783	0.456	0.334	-2.342	<0.05*
Control single	0.105	1.110	0.343	0.306	0.759
Mass	0.011	1.012	0.005	2.055	<0.05*

TABLE 4. Cox proportional hazard regression, estimating the effect of treatment on the time individuals remained uncaught during the medium-term vulnerability retest ($n = 115$; likelihood ratio test: 21.73, $df = 4$, $P < 0.001$). The control pairs treatment was used as a reference level. The number of events = 98 and refers to the total number of caught fish. Asterisks indicate significant differences ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$).

Parameter	Estimate	Exp (coef)	SE (coef)	Z-value	P-value
Direct exposure	-0.978	0.375	0.299	-3.266	<0.01**
Social exposure	-0.296	0.743	0.280	-1.054	0.291
Control single	0.357	1.429	0.298	1.196	0.231
Mass	-0.002	0.997	0.005	-0.508	0.611

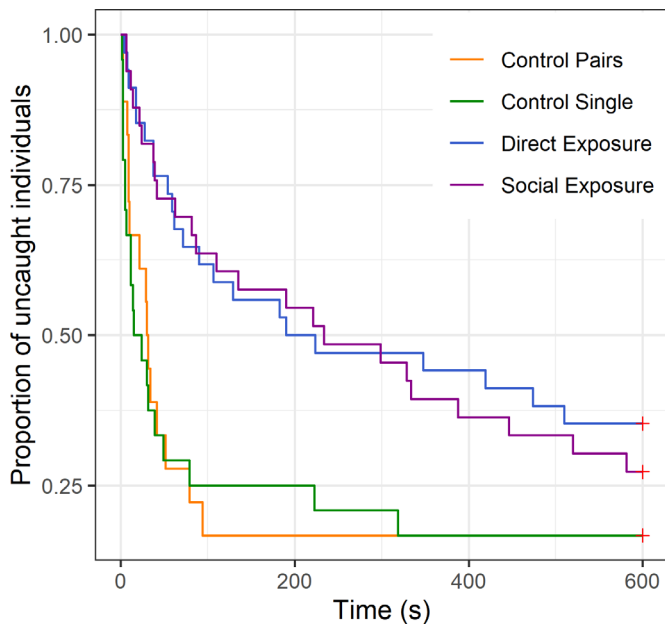


FIGURE 4. Survival curves illustrating the remaining proportions of uncaught individuals during the 600-s short-term vulnerability retest. The time (s) to ingest a corn-baited sham rig was used as a response variable for the corresponding treatments in control pairs (orange; $N = 18$), control single (green; $N = 24$), direct exposure (blue; $N = 34$), and social exposure (purple; $N = 33$). [Color figure can be viewed at afsjournals.org.]

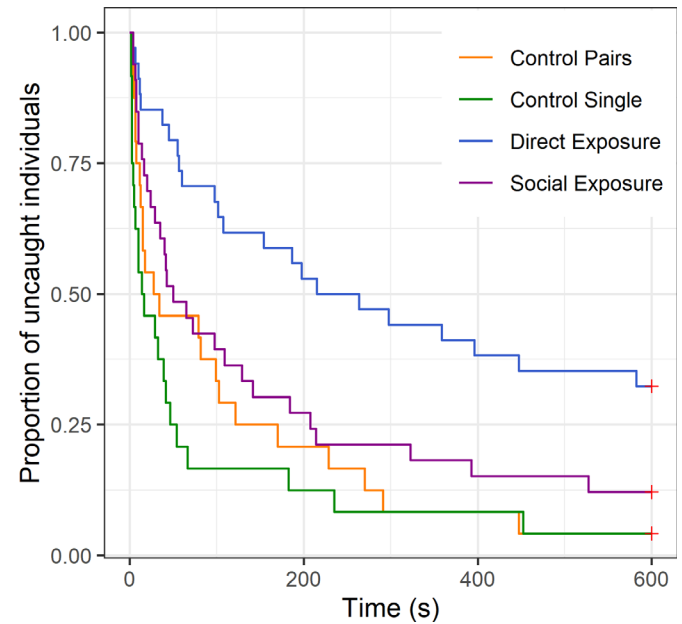


FIGURE 5. Survival curves illustrating the remaining proportions of uncaught individuals during the 600-s medium-term vulnerability retest. The time (s) to ingest a corn-baited sham rig was used as a response variable for the corresponding treatment in control pairs (orange; $N = 24$), control single (green; $N = 24$), direct exposure (blue; $N = 34$), and social exposure (purple; $N = 33$). [Color figure can be viewed at afsjournals.org.]

alone. These data indicate that not only fish with an actual direct hooking experience but also those with social exposure were able to discriminate against the angling rig, which is suggestive of social hook avoidance learning in Common Carp. Our work experimentally proves the observations reported in previous pond, lake, and tank studies that Common Carp (Klefoth et al. 2013; Monk and Arlinghaus 2017), and other species like Northern

Pike (Arlinghaus et al. 2017a, 2017b), can show hook avoidance behavior through social learning.

Our data constitutes the first experimental evidence of social hook avoidance in Common Carp that lasts at least 7 d postcapture. Previous studies on Largemouth Bass (Wegener et al. 2018; Louison et al. 2019b) and Rainbow Trout (Lovén Wallerius et al. 2019) failed to find evidence that social experience decreased hook avoidance in experimental settings. It is possible that the social threat

TABLE 5. Cox proportional hazard regression, estimating the effect of treatment on the time individuals remained uncaught during the 450-s vulnerability assessment with or without sham rig ($n=115$; likelihood ratio test: 27.09, $df=8$, $P<0.001$). The control pairs–corn first treatment was used as a reference level. The number of events=101 and refers to the total number of caught fish. For easier interpretation, the corresponding Figure 6 has been divided into the original angling treatments (denoted A, B, C, and D) and only compares sham or corn first between each treatment. Asterisks indicate significant differences ($P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$).

Parameter	Estimate	Exp (coef)	SE (coef)	Z-value	P-value
Social exposure–sham first	-1.367	0.254	0.450	-3.037	<0.01**
Social exposure–corn first	-0.845	0.429	0.447	-1.891	0.058
Control single–sham first	-0.011	0.988	0.457	-0.026	0.979
Control single–corn first	-0.697	0.497	0.452	-1.542	0.123
Control pairs–sham first	-1.242	0.288	0.454	-2.734	<0.01**
Direct exposure–sham first	-1.703	0.182	0.450	-3.243	<0.001***
Direct exposure–corn first	-1.451	0.234	0.447	-3.243	<0.01**
Mass	0.003	1.003	0.005	0.671	0.502

stimulus induced in Louison et al. (2019b) was not strong enough to foster social learning, thereby failing to promote a decline in catch rates for naïve observers. Specifically, Louison et al. (2019b) tested the response of naïve observers when stocked in ponds with demonstrators that had previously experienced catch-and-release angling, i.e., the study was based on (indirect) observational conditioning and the observer fish were not directly exposed to a demonstrator being captured. By contrast, the design used in this study (where a social individual observed the full range of a catch-and-release event) may suggest that individual fish need the whole range of social cues during a threatening angling situation to form an association between the lure and the various risk-related cues transmitted by the caught demonstrator to be able to respond appropriately in the future (Rendell et al. 2011).

In the study by Wegener et al. (2018), the authors derived their findings about the lack of social learning in Largemouth Bass by fitting statistical models to a time

series of catch rates and estimating catchability coefficients for group-held Largemouth Bass that experienced a hooking-and-release event and those that did not. While the caught-and-released subgroup of Largemouth Bass showed declining catchabilities over time, no such trend was observed for previously uncaught fish. While their study agrees with Louison et al. (2019b) that social learning to avoid angling is unlikely in Largemouth Bass, there are methodological issues that limit conclusive statements about whether social learning to avoid capture is possible in this species or not. For example, as all fish were held in groups in small replicated impoundments, the authors were not able to control which type of cues the various uncaught fish were exposed to during the catch-and-release angling sessions. It is, for example, possible that the uncaught fish encompassed a mixture of truly uncaught fish and fish that were hooked but managed to free themselves during the fight. Indeed, controlling for successful transfer of social cues in natural (whole lake or pond) settings is difficult due to both spatial and temporal scales (e.g., the experimenter cannot guarantee whether an observer is in the vicinity to detect a hooking event). Another limitation of Wegener et al. (2018) that is shared with the present research on Common Carp is that caught and uncaught fish might systematically differ in learning ability (as reported for Largemouth Bass; Louison et al. 2019a). The limitations identified for the previous studies cannot rule out that social hook avoidance learning does not exist in Largemouth Bass and Rainbow Trout. In both Wegener et al. (2018) and Louison et al. (2019b), catch rates of Largemouth Bass declined after only a fraction of the fish had been captured, which is suggestive that some form of social learning had taken place that negatively affected reactivity to the gear, unless most fish in the stocks were hooked and got lost prior to landing, as was the case in previous work with Common Carp (Beukema 1970a) and Northern Pike (Beukema 1970b). To conclude, we do not think that the available work rules out the possibility for social learning in species such as Largemouth Bass or Rainbow Trout. We instead highlight the importance for naïve observers to be subjected to the full range of threatening social stimuli, perhaps repeatedly, during a catch-and-release event to be able to form a negative association and develop hook avoidance behavior when confronted with dangerous lures.

The differences in reactions of omnivorous Common Carp relative to top predators, such as Largemouth Bass and Rainbow Trout, may also result from innate species-specific differences in foraging ecology, sociability, and communication. Common Carp are a highly social species (Huntingford et al. 2010) that feed in nonmobile benthos and have shown well developed learning capacities (Coble et al. 1985) compared with the more solitary top predators like Largemouth Bass (Wanjala et al. 1986) or Northern

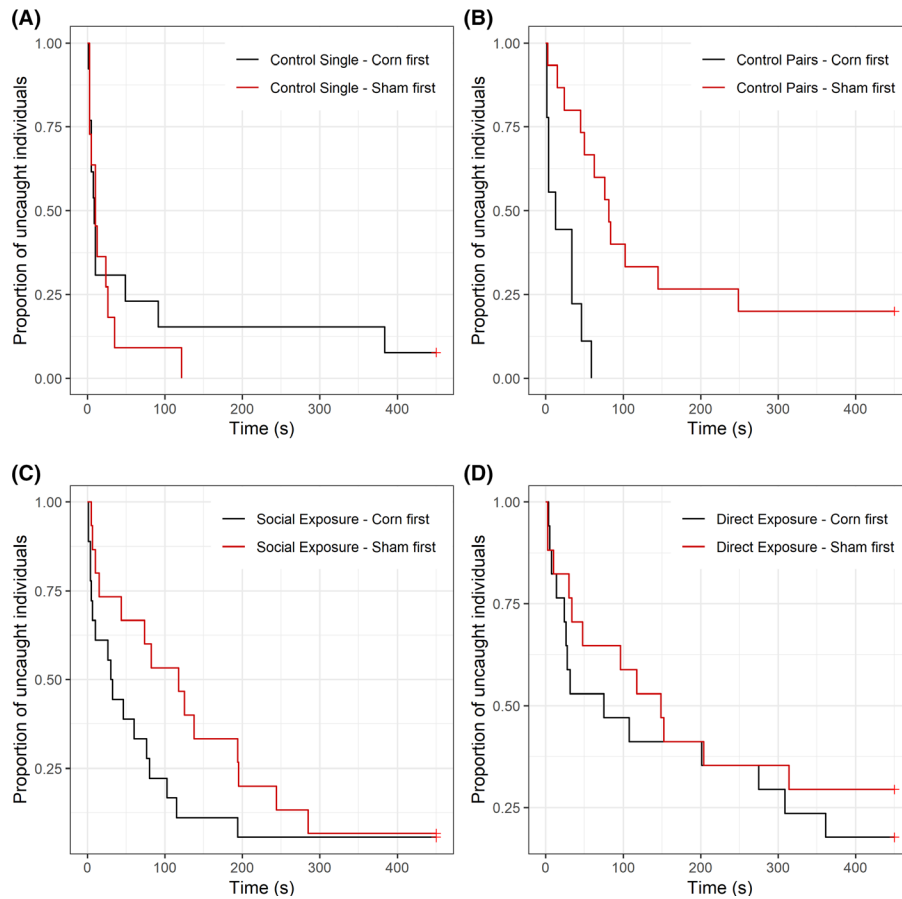


FIGURE 6. Survival curves illustrating the time (s) to ingest corn (corn first = black) or corn in the presence of a sham rig (sham first = red) in (A) control single ($N = 24$), (B) control pairs ($N = 24$), (C) social exposure ($N = 33$), and (D) direct exposure ($N = 34$) during the 450-s vulnerability assessment with or without sham rig. For easier interpretation, all angling treatments have been separated. [Color figure can be viewed at afs-journals.org.]

Pike, who are evolutionary adapted to forage with aggressive attacks on mobile prey. The different foraging adaptations of omnivorous fish like Common Carp and top predators like Largemouth Bass likely selected for differences in foraging mode and cognitive ability. This, in turn could have affected the ability to plastically learn from threat stimuli, which was found to be more expressed in omnivorous fish than in predatory fish (Coble et al. 1985). Relatedly, Alós et al. (2015) reported strong species-specific responses in angling vulnerability across a gradient from fully protected to exploited marine sites, indicating that different species respond differently to angling pressure through hook avoidance behavior. We propose that interspecific differences in cognitive ability and the overall intraspecific sociality of the species may dictate the propensity of a species to rely on social information derived from its conspecifics to avoid threatening situations (Coussi-Korbel and Frigaszy 1995).

The short-term vulnerability findings were not consistent over the medium-term vulnerability assessment 5 to 7 d after capture. During this time, the direct exposure of

catch-and-release angling was the only treatment that had retained the reduced angling vulnerability compared with all other treatments. A stronger effect of direct as opposed to social exposure was expected as the hooking induces a stronger physiological stress response (Woodward and Strange 1987; Pottinger 1998; Cooke et al. 2004; Meka and McCormick 2005; Arlinghaus et al. 2009; Rapp et al. 2012) than just observing hooking (Lovén Wallerius et al. 2019). Additionally, being personally injured is likely perceived as more harmful than just observing injury indirectly (e.g., through the release of Schreckstoff; Chivers and Smith 1998). An intensified harmful experience through direct hooking thus likely leaves a stronger cognitive legacy and may thus be remembered for longer than simply observing or otherwise sensing a conspecific that is struggling on the hook and is released. Indeed, a previous study in Rainbow Trout showed that the peak heart rate response of privately hooked individuals was initially higher than those only experiencing hooking indirectly through social cues (Lovén Wallerius et al. 2019).

In the medium-term vulnerability assessment, the previously decreased vulnerability observed in the social treatment was lost compared to the control pairs treatment, which constituted fish held initially in pairs. However, social exposure individuals were still significantly slower to ingest the angling gear compared with the control group held individually (control single). The fact that social exposure fish were still able to discriminate corn with and without a sham rig attached to it after 5 to 7 d is suggestive that Common Carp are capable of remembering a negative social stimuli within a few days. It will be an important question for future studies whether a single social hooking event would be remembered for longer time frames or get lost through fading memory over time. As recurrent negative stimuli may be important when shaping the learning response in fish with direct experience (Coble et al. 1985), repeated angling exposure (Koeck et al. 2020), an increase in magnitude of the stressor (Barton 2002), and the social learning mechanism (Brown and Laland 2003; Rendell et al. 2011) might affect whether or not decreased vulnerability will be retained in the social individuals for a longer time period.

The divergent response of the two control groups was initially unexpected and could be explained by habituation to the holding conditions, which in turn differentially affected the two control groups when tested individually for their first response to a bait. For example, individuals from the control single treatment could be perceived to be better habituated to the stress of being alone in a small aquarium (Barton 2002) and therefore might have been faster to ingest the angling bait in subsequent trials compared with the control pairs treatment. The stress of being kept alone for social fish (Portz et al. 2006) might also explain the results seen in the vulnerability assessment with or without sham rig, where individuals in the control pairs–sham first had a similarly decreased vulnerability as individuals in the social and direct exposures. Another possible explanation is that fish held jointly (as in the control pairs treatment) might have developed a fast response to the bait due to scramble competition previously reported in Common Carp (Huntingford et al. 2010). In turn, when held alone the same individuals might respond slower to the bait as the competitor was now missing from the test tank. Our work underscores that even subtle differences (e.g., holding individuals alone or in pairs) can affect their subsequent behavior and thus careful choice of control conditions is important to derive robust experimental findings.

Regarding the pretrial feeding data collected before the fish were exposed to angling, our results showed that individuals later assigned to the direct exposure ate more corn than social exposure individuals, suggesting an interindividual difference in readiness to take certain feeds (Bolnick et al. 2003; Pollux 2007). Sweet corn has in general been shown to be a preferred food item over pellets in a previous angling study on two different Common Carp genotypes, independent of

the individual vulnerability to capture (Klefoth et al. 2013). Therefore, it is unlikely that the initially decreased angling vulnerability in the social exposure treatment was caused by the generally lower preference for corn in the social exposure treatment compared with fish with direct experience. It is possible that the higher corn consumption for individuals later assigned to the direct exposure might indicate that these individuals had a different behavioral type (e.g., increased boldness fostering faster food intake; Klefoth et al. 2013, 2017), differed by levels of stress responsiveness (Koeck et al. 2019; Louison et al. 2019a), or were generally more dominant and monopolized the most easily accessible food source (Ward et al. 2003; Huntingford et al. 2010). This could also explain the observation that larger fish had an elevated food intake rate and thus increased angling vulnerability during the angling exposure, which has been reported across different species (e.g., Arlinghaus et al. 2008; Vainikka et al. 2016), including Common Carp (Klefoth et al. 2017). Moreover, a relationship among behavioral type (e.g., degree of boldness) and learning ability has been reported in fish (Lucon-Xiccato and Bisazza 2017), where shy fish (which were likely the ones assigned to the social treatment later) have shown greater learning retention ability towards a predator after 9 d compared with bold individuals (Brown et al. 2013). If this is the case, the long-term effects on catch rates due to direct hooking experience might be overestimated and the effects on catch rates due to social learning underestimated. In essence, the strength and type of the social learning mechanism (see Rendell et al. 2011) may influence catchability for longer periods than when fish are only exposed to direct hooking experience solely. An alternative view is that fish that are quick to learn are also more vulnerable to capture as recently shown experimentally in Largemouth Bass (Louison et al. 2019a). This would overestimate the rate of learning of directly hooked fish relative to the average individual in the population. More work in this area is needed to fully elucidate these possibilities and their effect on catch rates in relation to Common Carp and other species.

A limitation of our design is that the fish that were assigned to the direct exposure treatment were not randomly chosen (i.e., the fish that first ate the bait and got hooked became the directly exposed individual while the other conspecific was assigned to the social exposure). We choose this “self-selection” design of which treatment to become (either direct or social) over the alternative of experimental, manual hooking of randomly chosen fish because of concerns that manual hooking would create too much stress on all fish due to the increased handling time and that this practice would not transmit the same social and chemical cues to social individuals. This decision created the issue of nonrandom allocation of fish to either the direct or social treatment during the angling exposure. Yet, our design corresponds with natural conditions. A rich literature has shown that those fish that are

more vulnerable to angling are not a random set of the population (Philipp et al. 2009; Härkönen et al. 2014; Koeck et al. 2019), including previous work in Common Carp (Klefoth et al. 2017; Monk and Arlinghaus 2017). Instead, vulnerable and invulnerable fish differ in both physiological and behavioral as well as morphological traits (Lennox et al. 2017). In particular under seminatural holding conditions, variation among fish in stress responsiveness (Louison et al. 2017; Koeck et al. 2019) and personality (Härkönen et al. 2014; Klefoth et al. 2017) has repeatedly been shown to predict vulnerability to angling.

The strength of our work is its experimental nature, but whether our work equally applies to natural conditions remains uncertain. Common Carp usually feed in groups (Huntingford et al. 2010) and have been found to show strong evidence of social learning in food patch identification in the wild (Bajer et al. 2010). Therefore, our experimental design of testing vulnerability to hooking in isolation is artificial, as opposed to natural conditions, where it is more likely that groups of Common Carp exploit a food patch and demonstrators will jointly access food patches with naïve fish (Monk and Arlinghaus 2017). Video recordings associated with the paper of Klefoth et al. (2013) show that Common Carp as groups approach dangerous patches where previous hooking events took place with a predator inspection behavior and are able to spit out baited hooks without being hooked repeatedly. It is likely that social learning is much more pronounced with demonstrators around, and our experimental work needs further confirmation under more natural conditions to improve the ecological realism of the findings.

In conclusion, we provide experimental evidence that the social experience of angling can induce a plastic response that will decrease angling vulnerability in Common Carp in addition to the hook avoidance learning expected from direct hooking experiences. Direct hooking alone can explain the strong decrease in catch rates in catch-and-release fisheries reported across a range of species (van Poorten and Post 2005; Askey et al. 2006; Kuparinen et al. 2010; Klefoth et al. 2013; Arlinghaus et al. 2017a, 2017b; Monk and Arlinghaus 2017; Wegener et al. 2018; Lovén Wallerius et al. 2019; Koeck et al. 2020). Yet, an earlier essay (Meekan et al. 2018) suggested that in harvest-oriented fisheries, where the fish do not experience the negative stimulus of catch and release and are instead removed from the system for harvest, limited learning is to be expected, thereby aggregating the overfishing potential. Our work questions this hypothesis by providing evidence that at least Common Carp are also able to socially learn from observing or sensing other conspecifics be captured and develop a hook avoidance behavior. Altered vulnerability to angling at the population level within the realm of plastic learning can cause hyperdepleted catch rates (i.e., catch rates declining faster than

underlying abundance) (Arlinghaus et al. 2017a, 2017b; Alós et al. 2019). Such change in catchability will have major impacts not only on angler satisfaction but also on stock assessments using angler catch data (Alós et al. 2019). Yet, our findings are limited to just a few days and it is unclear for how long the direct and social experience will be retained. A recent study by Koeck et al. (2020) revealed that temporal closures might reset the vulnerability of Rainbow Trout, in turn increasing catch rates and population-level catchability. Therefore, for hyperdepletion to be commonplace in real fisheries, repeated catch and release might be required for social experience to affect whole-population catchability over a longer time period, for which there is observational evidence in Common Carp (Monk and Arlinghaus 2017). More studies are needed to evaluate if recurrent angling can induce a stronger social experience that can affect catchability in a more natural environment where social fish are surrounded by demonstrators and if the collective effects seen here have the potential to create a “timidity syndrome” (Arlinghaus et al. 2017a). Additional research is needed that considers other angling contexts and evaluates similar questions among a wide range of relevant fish targeted by anglers.

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