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Reexamining one-trial learning in common carp (*Cyprinus carpio*) through private and social cues: No evidence for hook avoidance lasting more than seven months

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ABSTRACT

When a fish is caught by angling and released, it is unclear for how long that fish will be able to remember the experience and exhibit hook avoidance. Previous research in ponds using carp (*Cyprinus carpio*) as a model have suggested that in this species a single hooking event might be enough to cause hook avoidance to last over one year. We re-examined this finding, determining whether private (i.e., personal experience of a catch-and-release event) or social (i.e., sensing a conspecific being hooked and released) hooking experiences maintains hook avoidance 7 and 14 months from the initial experience. A fully controlled laboratory experiment was used that recorded the behavior towards sham-rigs where the hook tip was removed, which served as measure for hook avoidance. Although individuals with a private hooking experience required more time to pick up the sham rig 7 months after the initial hooking relative to controls, no differences in ultimate ingestion rates over a time period of 600 s were found, indicating a more cautious approach to the hook but the loss of hook avoidance after 7 months. For carp with a one-trial social hooking experience, neither an increased latency to ingest the offered sham rig nor differences in ingesting rates compared to never-hooked controls were found, indicating that the carp had forgotten that experience after about half a year. Thus, the previous findings from pond studies with group-held carp according to which one-trial hooking is enough to reduce the capture probability one year after the event could not be replicated in carp tested alone in the laboratory. It is unclear whether strain differences, lack of statistical power or differences in the set up alone or in combination explain the differences in study outcomes.

1. Introduction

Fish can learn through their own experiences (i.e., private learning) and from socially acquired information provided by conspecifics (i.e., social learning) (Dill, 1983; Kieffer and Colgan, 1992; Brown and Laland, 2011). Social learning is beneficial as it allows for a more rapid information spread among individuals than if learning was only possible through private experiences (Sumpter et al., 2008; Brown and Laland, 2011). This phenomenon has been well documented in the context of antipredator behavior (Griffin, 2004). Recreational fishing - one widespread form of human-induced predation threat – also emits stimuli to which fish might respond through learning. Globally, only about one-third of the recreational catch is used for human consumption and the remainder is released alive (i.e., catch and release, C&R; Cooke and

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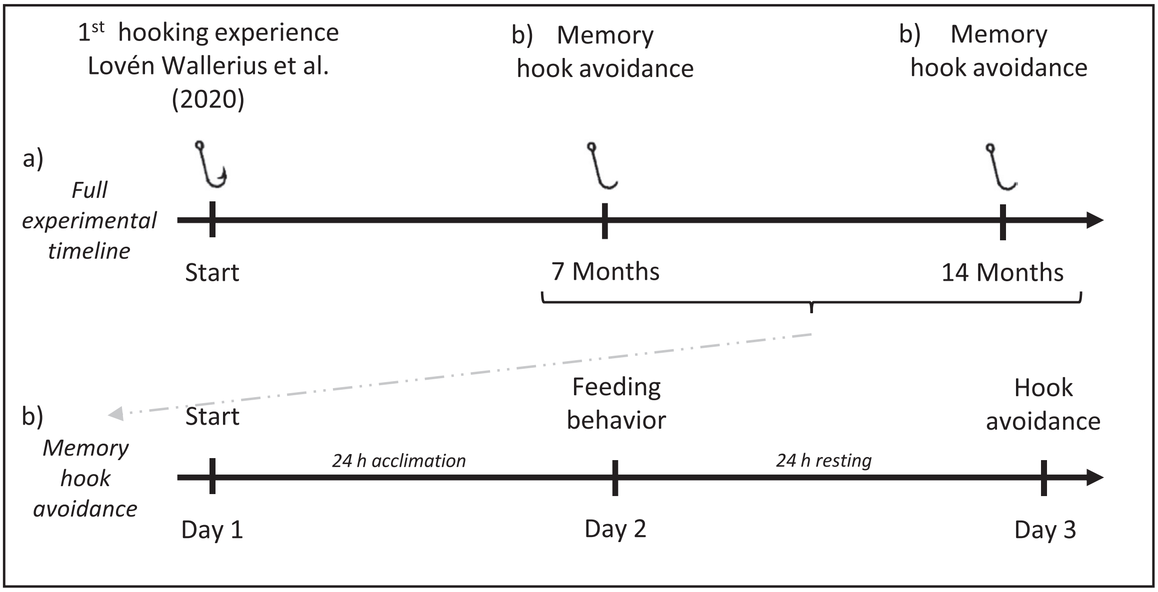

Fig. 1. Overview and timeline of the angling experiments. Panel a) shows the full experiment timeline over 14 months starting after the 1st hooking experience, panel b) the testing procedure for memory retention on hook avoidance and food aversions at month 7 and 14.

Cowx, 2004). The hooking experience during C&R can result in individual learning to reduce or avoid future recapture, either through private or social cues (Beukema, 1970a, 1970b; Clark, 1983; Raat, 1985, 1987; Louison et al., 2019). Hook avoidance behavior has been documented in a wide range of species, such as largemouth bass (*Micropterus salmoides*) (Philipp et al., 2009; Louison et al., 2019), rainbow trout (*Oncorhynchus mykiss*) (van Poorten and Post, 2005; Askey et al., 2006; Lovén Wallerius et al., 2019), northern pike (*Esox lucius*) (Beukema, 1970a), silver seabream (*Pagrus auratus*) (Gilbert et al., 2001), lemon sharks (*Negaprion brevirostris*) (Spaet et al., 2010), goldfish (*Carassius auratus*) (Chen and Zeng, 2022) and common carp (*Cyprinus carpio*) (Beukema, 1970b; Beukema and de Vos, 1974; Raat, 1985, 1987; Klefoth et al., 2013; Lovén Wallerius et al., 2020).

Field studies have shown that catch rates of entire populations of fish rapidly declined after the onset of C&R fishing when only a fraction of the entire stock was hooked at least once (Beukema, 1970a, 1970b; Raat, 1985, 1987; van Poorten and Post, 2005; Askey et al., 2006; Klefoth et al., 2013; Monk and Arlinghaus, 2017). Such rapid declines in catches are indicative of social learning in response to C&R fishing, which has been suggested or implied in a range of species (Beukema, 1970a; b; van Poorten and Post, 2005; Lovén Wallerius et al., 2019; Chen and Zeng, 2022), including common carp (Beukema, 1970b; Raat, 1985, 1987; Klefoth et al., 2013; Monk and Arlinghaus, 2017). Experimental evidence for social learning of hook avoidance in freshwater fishes has recently been documented for carp by Lovén Wallerius et al. (2020). Other empirical tests designed to show socially learned hook avoidance failed to provide convincing results in largemouth bass (Wegener et al., 2018; Louison et al., 2019), goldfish (Chen and Zeng, 2022) and rainbow trout (Lovén Wallerius et al., 2019). The well-developed cognitive abilities of carp relative to other freshwater fish (Coble et al., 1985), combined with high sociability during foraging (Bajer et al., 2010), may facilitate social hook avoidance in this species.

Fish are known to remember threats and maintain aversive behaviors for several days (Davis and Agranoff, 1966; Croy and Hughes, 1991; Brown and Smith, 1998; Brown et al., 2011; Kimber et al., 2014) to several months (Csányi et al., 1989; Zion et al., 2011; Triki and Bshary, 2020). The hooking experience and associated handling (e.g., air exposure) has the potential to induce sub-lethal physiological impairments (Cooke et al., 2013) and may manifest in aversive behaviours, such as locomotor changes (Cooke et al., 2000), altered foraging (Stålhammar et al., 2012), changes in nest side choice and nest site fidelity in nest-guarding species (Twardek et al., 2017) or seeking safer habitats (Klefoth et al., 2008, 2011). However, fish may remember certain negative experiences just for a limited time, with the length of memory scaling with cognitive ability, the degree of noxious stimulation, the severity of the threat (Bintz, 1971; Gallon, 1972; Dunlop et al., 2006) and the rate of environmental change (Kotrschal and Taborsky, 2010). Fish have been documented to forget threatening stimuli, with forgetting times varying from 8 to 55 days without reinforcement (Croy and Hughes, 1991; Kimber et al., 2014; Zion et al., 2011). It is likely that a fish will remember a private hooking experience longer than a social one, as the private experience should stimulate more harm than just a social exposure to an angling event. Indeed, Lovén Wallerius et al. (2019) observed increased heart rates in trout in response to both private and social angling experiences as a physiological stress response, with only the private experience reducing angling vulnerability to subsequent angling trials.

In the case of carp, the literature is inconsistent in how long this species can remember a one-trial hooking experience. Beukema (1970b) revealed hook avoidance for up to one year in pond experiments with group-held carp after a single contact with a fishing hook. By contrast, Raat (1985) reported a loss of hook avoidance after one year in pond experiments with carp. In both studies, methodological issues, such as conducting the experiments in large ponds with conspecifics, prevented the possibility to track individual fish and their capture histories. Therefore, in the above-cited studies the researchers were unable to identify the exact cues that individual carp needed to develop hook avoidance, and the question remains to what extent not only a private but also a social hooking experience may affect the long-term memory of a previous hooking event in carp.

Our objective was to investigate the hook avoidance behavior of common carp 7 and 14 months after a first C&R event. Specifically, our aim was to compare how a private experience after a single hooking event and the social experience of observing the hooking event of a conspecific would influence hook avoidance behavior in future angling events. To address these objectives, we used carp that had experienced private or social angling exposure in a former C&R experiment, in which it was reported that privately and socially acquired hook avoidance behavior was present in the first few days after the C&R event (Lovén Wallerius et al., 2020). We tested the hypotheses that I) carp with a private hooking experience exhibit a lower vulnerability to angling compared to fish with a social hooking experience at least one year after

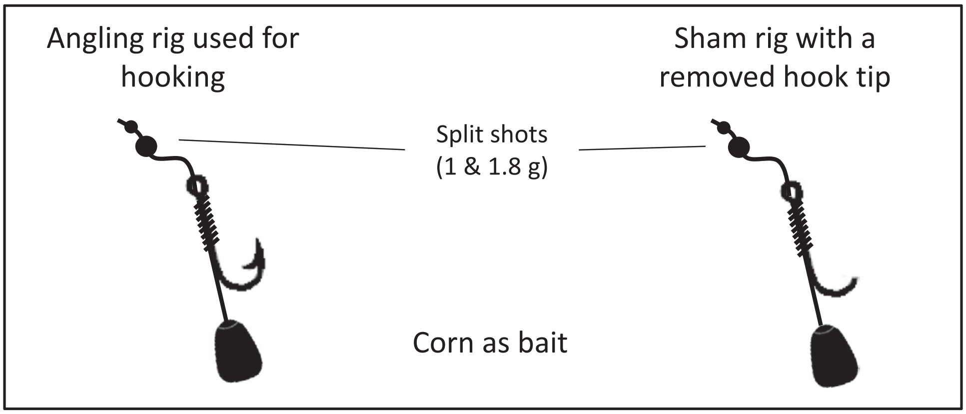

Fig. 2. Comparison between the angling rig used for hooking and the sham rig (removed hook tip to avoid further hooking experiences). Presenting the bait underneath the hook allows the hook to find hold in the front part of the fish mouth, which causes negligible injuries and is a common method in carp fishing (Rapp et al., 2008). The two split shots were used as weights and sweet corn as bait.

the initial exposure to hooking and release (Beukema, 1970b), II) due to fading memory, the impact of a one-trial private and social hook avoidance behavior decreases over time and eventually vanishes (Raat, 1985).

2. Methods

2.1. Overview

We conducted three-day angling experiments 7 and 14 months (Fig. 1a) after the study fish experienced either a single private or social hooking event as documented in Lovén Wallerius et al. (2020). We thereby retested the original treatment fish developed by Lovén Wallerius et al. (2020) on memory retention of hook avoidance (Fig. 1).

2.2. Original treatment fish varying in private or social hook experiences

The carp that we used in our experiments were survivors of the early C&R/hook avoidance experiments of Lovén Wallerius et al. (2020). All experimental carp were initially angling-naïve and originated from pond aquaculture. All subsequent angling experiments both by Lovén Wallerius et al. (2020) and in the present study were conducted in a temperature-controlled laboratory environment, where fish were held in large tanks (1 m × 1 m × 0.7 m; Length × Width × Depth), and experiments conducted in small aquaria in three immediately neighboring, but separated recirculating filter systems, each consisting of eight aquaria (45 liters; 50 cm × 30 cm × 30 cm, Length × Width × Depth). This setup allowed for the recording of carp behavior in a maximum of 24 aquaria simultaneously. All aquaria were equipped with a large stone, a plastic plant and an air stone to provide cover and oxygen for the fish. During all experiments, both side panels of the aquarium were covered with a styrofoam panel to avoid visual contact between fish in the neighboring aquaria, and the freshwater inflow was paused ten minutes before the experiments began to avoid chemical communication across aquaria. The experimental fish varied by angling experience and were initially established by Lovén Wallerius et al. (2020) as follows:

1) Private & Social: two angling-naïve carp were kept in one aquarium and exposed to an angling rig baited with commercially bought sweet corn (Bonduelle, Reutlingen, Germany) (Fig. 2). The angling rig consisted of a 15 cm braided line (10 kg breaking strength) and two split shots (1 g & 1.8 g) as weights attached 5 cm behind the hook (Gamakatsu, microbarbed, size 14). The braided section was tied to a 1.5 m monofilament nylon line (diameter: 0.25 mm; 3.85 kg breaking strength) to ease removing the rig out of the aquaria. The first fish getting hooked within 600 s was kept on the line for 30 s, netted and air exposed for 30 s to remove the hook and released back into the same aquarium, and became the "Private" fish with a direct C&R experience. The observing carp became the "Social" treatment, who had an indirect hooking experience by being exposed to visual and chemical cues (e.g., Schreckstoffe; Chivers and Smith, 1998) of a struggling carp on the line and the subsequent release of the hooked fish into the same aquarium.
2) Controls: two carp were kept paired in one aquarium of the same dimension within the same recirculation system as above, while a corn baited up sham rig (Fig. 2) was presented similar to 1) but without a sharp hook. Hence, the sham rig was the very same rig as used for the treatment assignments, with the difference that the hook tip was removed. The control fish thus received no hooking or angling experience.

All fish had a uniquely-coded PIT-tag (11 mm; Oregon RFID, Portland OR, USA) implanted into the body cavity by Lovén Wallerius et al. (2020) and were thus individually identifiable. Between the first angling experiments (Fig. 1a) conducted by Lovén Wallerius et al. (2020) (who generated treatment fish with a one-trial private and social hooking experience) and the present study, the carp were kept outdoors for 7 months in an earthen pond (13 m × 6 m × 1 m; Length × Width × Depth) and fed by conventional fish pellets (Ø = 2 mm; Aller Aqua, Golßen, Germany). The fish were transferred back in spring 2018 (April/May) into the same climate-controlled room where Lovén Wallerius et al. (2020) had conducted the first hook avoidance experiments. After draining and careful netting out of the holding pond, the fish were equally distributed into four, oxygen aerated, recirculation holding tanks (1 m × 1 m × 0.7 m; Length × Width × Depth) in the laboratory. Here, the carp were kept for the next 7 months within the recirculation holding tanks except when used for the experiments. The systems were located in a climate-controlled room to maintain a near constant water temperature of 17 ± 0.5 °C and a timer regulated lighting (12 h per day) to simulate day/night, which both minimized any seasonal behavioral effects in the immature study fish during our angling experiments. The water quality (pH, oxygen content, temperature) was monitored with a multi-parameter probe (WTW, Weilheim, Germany) before and during the experiments. While keeping the fish in the holding tanks, the carp were fed every second day with the same fish pellets as used in the ponds, except the day before the actual experiment to increase the likelihood that they would ingest the offered items rather than being satiated. All tested fish were in good condition, and a regular food supply was ensured both during the holding phase and during the experiments.

2.3. Memory testing of hook avoidance 7 and 14 months after the first hook and release event

In the present study, due to natural mortality, 60 of originally 91 experimentally carp (Private: N = 20; Social: N = 22; Control: N = 18) were examined for individual hook avoidance and memory retention 7 and 14 months after the initial hooking experience (Fig. 1a). Individual carp were randomly allocated into 24 aquaria (45 liters; 50 cm × 30 cm × 30 cm, Length × Width × Depth) using the PIT tag ID for identification. When the behavior of the fish was not recorded within the respective experiment, styrofoam panels were set in place in a way that visual contact between two neighboring aquaria was possible, which appeared to calm the fish. Moreover, freshwater inflow was provided and a black tarp was hung to cover the front of all aquaria to minimize external disturbance until the next day.

After a 24-hour acclimation period, a feeding experiment was conducted on day two (Fig. 1b). Each carp was exposed to three sweet corn kernels and three fish pellets randomly dropped either left or right into the aquarium. Through this approach, we tested if an aversion of conventional sweet corn kernels took place due to the previous use as bait during the original angling trials 7 and 14 months ago (Lovén Wallerius et al., 2020) or if non-threatening fish pellets that were never associated with hooking during the life of the carp were preferred. The behavior of four fish was recorded simultaneously for 600 s with webcams (Logitech C920), while the number of consumed corn kernels and fish pellets as well as which item was ingested first was measured. In case no food item was ingested, the food "preference" was assigned as "no food". This experiment was based on an adapted method to predict food preferences in carp developed by Klefoth et al. (2013).

On the following day three (Fig. 1b), the hook avoidance behavior was evaluated by measuring the time to pick up a corn baited sham rig (Fig. 2) for the first time within 600 s. This sham rig setup was used before by Lovén Wallerius et al. (2020). We estimated two measures of hook avoidance – the speed of approaching the bait and ultimately whether the bait on the sham rig was uptaken or not into the mouth.

After all experiments on day three were completed (Fig. 1b), each carp was gently netted out of the aquarium and the total length (TL to mm) and weight (Sartorius, Sartorius AG, Göttingen, Germany; accuracy ± 0.1 g) were measured (7 months: weight, mean ± SD = 73.3 ± 26 g; total length, mean ± SD = 16.7 ± 1.9 cm; 14 months: weight, mean ± SD = 157.2 ± 60.6 g; total length, mean ± SD = 21.6 ± 2.7 cm), before being transferred into an empty holding tank within the climate-controlled room. The random allocation to the treatments revealed a similar size and weight distribution among the treatments in the retests using one-way ANOVAs (7 months: weight $F_{(2, 57)} = 1.482$, $p = 0.236$, total length $F_{(2, 57)} = 1.935$ $p = 0.15$; 14 months: weight $F_{(2, 57)} = 2.061$, $p = 0.137$, total length $F_{(2, 57)} = 2.987$, $p = 0.06$). The identical sequence and experiments were performed 7 and 14 months after the first hooking experience (Fig. 1b).

2.4. Analysis

Using Pearson's chi-squared tests, the aversion or the preference to a food item (first ingested item: corn vs. pellet vs. no food) within the feeding experiment was compared across the treatments at month 7 and 14. Differences in the number of corn kernels or fish pellets eaten between the treatments were examined with generalized linear models (GLM, Poisson distribution for count data; using the "glm" function in R) with treatment and total length of each fish serving as co-variates.

Cox proportional hazard regressions ("coxph" function of the survival package in R; Therneau et al., 2021) right censored at 600 s were used to test for differences in time to pick up the sham rig for the first time between the treatments in all time periods. All calculated models met the proportional hazard assumptions ("cox.zph" function; $p > 0.05$), and homogeneity of variances ($p > 0.05$) was tested using Levene's tests. Additionally, total length was included as time-independent covariate. Each event (i.e., first uptake of the sham rig) was scored as a binary variable (1 = event, 0 = no event) as the regression models always account for one event per individual and were tested for significance at an alpha value of 0.05. We will interpret results of the Cox regressions as indicators of vulnerability to hooking as it measures the time to approach and ingest the sham rig. Thus, a fish picking up the bait earlier will have a higher vulnerability to fishing during scramble competition among groups of carp.

The Cox proportional hazard regressions measure the time to the event (i.e., pick up of the sham rig). From a fitness perspective, the time dimension may be less relevant and only the ultimate binomial outcome (corn baited sham rig picked up or not) may matter. We thus additionally estimated logistic regression models with generalized linear models (GLM, binomial distribution "logit") and examined the same predictor variables as in the Cox proportional hazard regressions. We call the outcome of the logistic analysis hook avoidance because the ultimate fate (to pick up the bait or not) within 600 s was modelled as dependent variable. All statistical analyses were performed using the software R version 4.1.2 (R Core Team 2022).

Table 1
Average time, standard deviation and median of the time to pick up the sham rig within 600 s 7 and 14 months after the initial hooking experience among treatments. The fraction of captured individuals shows the percentage of individuals that ingested the offered sham rig within 600 s, while the fraction of uncaptured fish shows the percentage of individuals that did not ingest the offered sham rig within 600 s.

Treatment	Average time [s]	SD [s]	Median [s]	Fraction of captured fish	Fraction of uncaptured fish
7 months					
Control	151.6	224.2	33.5	83.3 % (n = 15)	16.7% (n = 3)
Private	287.3	258.8	169.8	65.0 % (n = 13)	35.0% (n = 7)
Social	193.5	213.6	126.5	90.9 % (n = 20)	9.1% (n = 2)
14 months					
Control	266.6	277.9	89.8	61.1 % (n = 11)	38.9% (n = 7)
Private	378.5	262.9	587.8	50.0 % (n = 10)	50.0% (n = 10)
Social	380.4	267.2	600.0	45.5 % (n = 10)	54.5% (n = 12)

3. Results

3.1. Vulnerability to hooking and hook avoidance after 7 months

At month 7 after the initial experiment of Lovén Wallerius et al. (2020), carp from the control treatment required on average 152 s to ingest the sham rig, while fish with a private hooking experience waited nearly twice as long before, ingesting the lure after, on average, 287 s compared to controls (Table 1). Although the time required to ingest the offered sham rig was significantly longer for privately hooked fish relative to control fish (54 % longer, $p = 0.04$) with no previous hooking experience (Cox proportional hazard regressions, Fig. 3a, Table 2), indicating reduced vulnerability to hooking in private fish, no statistically supported differences in final hook ingestion rates ($p = 0.13$) of carp with a private hooking experience (Logistic regressions, Fig. 4a, Table 3) were found. The latter finding indicated that the private fish had lost their ability to avoid being hooked by month 7, indicating memory loss of hook avoidance at this time period. Fish with a social hooking experience needed an average of 194 s to pick up the sham rig, and did not differ in the latency to pick up the sham rig ($p = 0.67$) (Fig. 3a, Table 2) nor in terms of hook ingestion rates ($p = 0.42$) compared to control fish (Fig. 4a, Table 3). Therefore, memory loss of the initial social hooking experience 7 months ago resulted in a similar

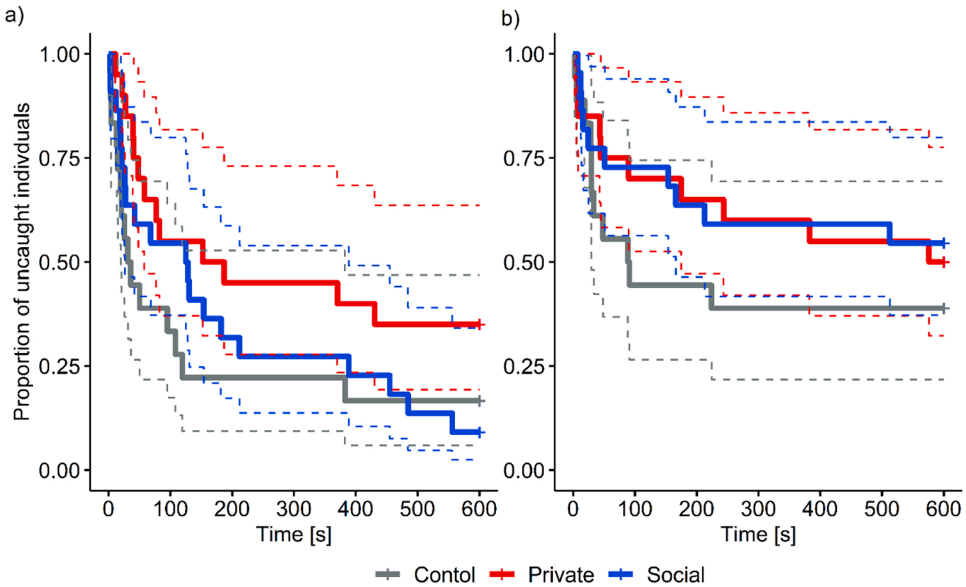

Fig. 3. Time to event graphs (i.e., first uptake of the sham rig) illustrating the proportion of uncaught individuals in each treatment 7 (a) and 14 (b) months after the initial hooking experience. Observation time was 600 s. Dashed lines indicate the 95 % confidence interval.

Table 2
Cox proportional hazard regression model comparing the time to pick up the sham rig 7 and 14 months after the initial hooking experience among treatments. The "Control" treatment was used as reference level. Asterisks indicate significant differences (p < 0.05 *; p < 0.01 **; p < 0.001 ***).

Factor	Estimate	Exp (coef)	SE (coef)	*p*-value
7 months				
Private	- 0.78	0.46	0.38	0.04 *
Social	- 0.15	0.86	0.34	0.67
Total length	- 0.10	0.91	0.08	0.24
14 months				
Private	- 0.35	0.70	0.45	0.43
Social	- 0.53	0.59	0.45	0.24
Total length	0.04	1.04	0.07	0.56

7 months: N = 60; likelihood ratio test: 5.86, df = 3, p = 0.1; number of events = 48
14 months: N = 60; likelihood ratio test: 1.69, df = 3, p = 0.6; number of events = 31

vulnerability to hooking and a similar hook avoidance of social fish relative to control fish.

3.2. *Vulnerability to hooking and hook avoidance after 14 months*

At month 14 after the initial experiment of Lovén Wallerius et al. (2020), carp with a private hooking experience required a mean of 379 s and fish with a social hooking experience a mean of 380 s to ingest the sham rig compared to controls with an average time of 267 s (Table 1). Despite the longer latency to pick up the sham rig of carp with a private and social hooking experience, both treatments showed no significant differences in the time to pick up the sham rig (Private: $p = 0.43$; Social: $p = 0.24$) (Fig. 3b, Table 2) and ingestions rates (Private: $p = 0.53$; Social: $p = 0.31$) (Fig. 4b, Table 3), indicating the loss of hook avoidance behavior by month 14.

3.3. *Food preference and total length impacts on vulnerability to hooking and hook avoidance*

Neither carp with a private nor with a social hooking experience showed any food preferences or differences in the amount of consumed food items (corn or pellet) compared to control fish at month 7 and 14 (Tables A1, A2, A3). Further, neither the time to pick up the sham rig or the ingestions rate of the sham rig were significantly related to total length of carp (Tables 2, 3).

4. Discussion

Our study did not support the early findings by Beukema (1970b) who reported that a single hooking experience lead carp to become more difficult to catch in subsequent angling situations and that this behavior is retained over a year after a previous hooking experience. Although fish with private hooking experience required significantly longer time to ingest the sham rig compared to controls (which we interpret as lower vulnerability to subsequent re-capture), the ultimate hook ingestion rates did not differ at month 7, indicating a memory loss of the formerly acquired hook avoidance behavior that was described in Lovén Wallerius et al. (2020) for the first few days after initial C&R. Moreover, we found that the consequences of a hooking experience were much more pronounced when exposed to a private compared to a social experience, as socially hooked fish neither showed an increased latency to ingest the sham rig nor differed in ingestion rates compared to control fish 7 months after the experience. Therefore, our work supports Raat (1985) and is in contrast with Beukema (1970b) in that a one-trial hook experience is insufficient to generate significantly reduced hook avoidance after one year, as no statistically supported differences in the ultimate uptake of the sham rig within 600 s of exposure either 7 or 14 months after the initial hooking event were found. Collectively our work demonstrated that the effects of hooking were much less pervasive and were forgotten ~7 months after the initial exposure to hooking in a sample of carp held in the laboratory and tested individually.

Previous work in carp has shown that hooking creates hook-shy fish within a few days of time (Beukema, 1970a, 1970b; Raat, 1985, 1987; Klefoth et al., 2013; Lovén Wallerius et al., 2020), and our works suggests that carp that experienced an actual C&R event continued to show evidence of increased hook shyness after 7 months, but this behavior was not sufficient to completely avoid being hooked at similar rates as angling-naïve controls. Hook avoidance behavior most likely results from the physical contact with a fishing hook coupled with a physiological stress response during the hooking event that is perceived as stress- and harmful. The fact that angling induces physiological stress impairments is known from a voluminous body of work (e.g., Arlinghaus et al., 2009; Rapp et al., 2012, 2014; Cooke et al., 2013; Lovén Wallerius

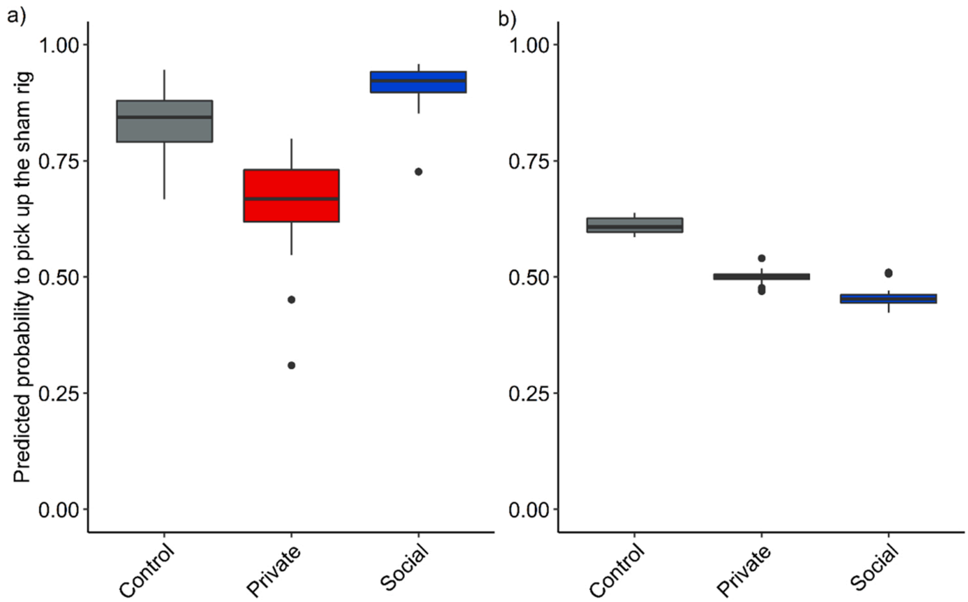

Fig. 4. Boxplots illustrating the predicted probability to pick up the sham rig within 600 s for each treatment 7 (a) and 14 (b) months after the initial hooking experience.

Table 3
Logistic regression models (GLM, using binomial distribution "logit") comparing the ingestions rates of the sham rig within 600 s at 7 and 14 months among treatments. The "Control" treatment was used as reference level. Asterisks indicate significant differences ($p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***).

Coefficients	Estimate	SE	Z-value	*p*-value
7 months				
(Intercept)	6.35	3.32	1.91	0.06
Private	- 1.28	0.84	- 1.52	0.13
Social	0.80	0.99	0.81	0.42
Total length	-0.28	0.19	-1.48	0.14
14 months				
(Intercept)	- 0.18	2.30	- 0.08	0.94
Private	- 0.42	0.67	- 0.63	0.53
Social	- 0.66	0.65	- 1.01	0.31
Total length	0.03	0.10	0.28	0.78

et al., 2019; Hlina et al., 2021) and implies that the hooking experience itself is an exhausting, energetically demanding and stressful experience for fish (Cooke et al., 2002; Arlinghaus et al., 2007). Although our work revealed a similarly prolonged latency to ingest the sham rig compared to the earlier experiments on the same study fish a few days after exposure (by 56.9–62.5 %; Lovén Wallerius et al., 2020), carp with a previous private hooking experience ingested the sham rig with the same probability as control fish, which indicated the loss of hook avoidance already at month 7. Depending on the severity of the particular hooking event, angling-related stressors will manifest in behavioral changes that can require several days to recover from (e.g., Cooke et al., 2002; Klefoth et al., 2008, 2011; Henry et al., 2009; Ferter et al., 2015; Arlinghaus et al., 2008, 2017; Lovén Wallerius et al., 2020). In carp specifically, post-release movement alterations have not been reported after a recovery phase of about one day in the wild (Rapp et al., 2012, 2014), suggesting that carp are quite resilient to angling-induced stressors. Thus it is possible that although the initial experience may be assumed as a negative stimulus (Lovén Wallerius et al., 2020), it was not lasting and harmful enough to associate similar events with the accompanying stressors for several months in the future. It is of course also possible that cognitive limitations prevented the carp from remembering the aversive stimulus of the initial hooking and release event. However, the fact that the time to approach the bait was significantly longer in privately hooked carp 7 months after the initial event suggest some level of remembering of the hook was cognitively achieved, but it was not strong enough to fully prevent the hook uptake.

Situations associated with a stressful, harmful or negative experience can be remembered by most vertebrates and often drive preventive behaviors like avoiding certain areas or objects in future situations associated with the negative experience (Ferrari et al., 2005; Gerber et al., 2014). Accordingly, it is conceivable that the study carp learned to associate certain negative experiences, most likely the hooking event, with a respective stress response and attempted to avoid a similar experience within the first few days after the initial experience (Lovén Wallerius et al., 2020) by avoiding the hook uptake through spitting and sorting processes (Sibbing et al., 1986) as revealed in video documentaries in this species when encountering hooks (Klefoth et al., 2013). It is important to note that not all fishes show aversive behavioral change to hooking. Predatory fishes such as Atlantic cod (*Gadus morhua*) and pike have been found to be physiologically and behaviorally unaffected by hooking related injuries (Eckroth et al., 2014; Pullen et al., 2019). In comparison, carp are generally better learners than predatory freshwater fish (Coble et al., 1985), which might explain the species-specific variation and the ability to show hook avoidance for at least a few days in carp and the reduced vulnerability to ingest a hook lasting at least 7 month in this species.

Relative to carp with a private hooking experience, memory loss also started in carp with a social hooking experience prior to the experiments at month 7, as we observed no signs of altered vulnerability (i.e., prolonged latency to ingest the sham rig compared to control fish) or hook avoidance (i.e., reduced ingestion rates or) 7 and 14 months after a one-trial social hooking experience. By contrast, Lovén Wallerius et al. (2020) reported that carp with a social experience required significantly longer to pick up the sham rig (by 54.4–56.6 %) compared to control fish two hours after initial experience. The fact that we failed to statistically detect hook avoidance after 7 and 14 months in fish with a one-time social hooking experience suggests that this experience was forgotten after a few months. Therefore, our and the work by Lovén Wallerius et al. (2020) tentatively suggests that individuals socially experiencing a hooking event can associate the sham rig with a negative stimulus (i.e. indirect hooking experience), but remember this only for minimum a few days after the social experience.

In previous studies, socially learned hook avoidance was often put forth as an explanation for declining catch rates for uncaught fish in group trials (e.g., Beukema, 1970b; Raat, 1985; Klefoth et al., 2013; Koeck et al., 2019, 2020; Lovén Wallerius et al., 2020) or in angling experiments in the wild (van Poorten and Post, 2005; Askey et al., 2006; Kuparinen et al., 2010; Arlinghaus et al., 2017). For example, Beukema (1970b) reported that after initial high catch rates on the first days, the catchability of carp decreased rapidly and it became harder to catch previously uncaught carp. A reduced catchability of a small carp population after only a fraction of the fish were captured was also reported by Klefoth et al. (2013) in ponds. Monk and Arlinghaus (2017) similarly described rapid declines in catch rates in a study with tracking carp in the wild shortly after the onset of angling and after only a few carp were captured. Although these effects are suggestive for social learning, it was not possible to control all socially transmitted information each individual fish received during a C&R event. For instance, Beukema (1970b) reported high losses after hook setting during experimental angling in a pond, which increased the chance that fish were falsely assigned to a social experience where those fish received a hooking experience but were not landed. In our work, we kept track of individual fish with a private and social hooking experience and failed to find evidence for retention of social hooking experiences 7 and 14 months after a one-trial event. It is possible that the results would differ in more natural fishing situations as running carp through a laboratory experiment might alter behaviors and direct attention away to deal with the artificial environment. Ideally, experiments should be repeated in groups with high resolution tracking allowing to identify each individual fish and what experiences they have been subjected to.

Similar to other studies that failed to find social hook avoidance in other fish species (Wegener et al., 2018; Louison et al., 2019; Lovén Wallerius et al., 2019; Chen and Zeng, 2022), it could be that the social cue transmission during our experimental hooking was not sufficient to maintain a socially learned hook avoidance behavior in the long term. That an insufficient transmission of social stimuli might be responsible for the absence of social learning has already been described for largemouth bass in Louison et al. (2019), while testing angling-naïve fish together with angling-experienced demonstrators, where the angling-naïve fish had never actually observed a hooking experience. Similar findings were reported in experiments with goldfish, in which visual stimuli without the transmission of chemical information during a social hooking experience did not result in being less vulnerable to angling (Chen and Zeng, 2022). Although our study fish received the full range of chemical and visual stimuli during the initial hooking experience (Lovén Wallerius et al., 2020), our work tested social fish in isolation. Perhaps, social fish need to observe the behavior of private fish related to a bait, for the memory of social fish to be "triggered" and hook avoidance be shown in response (Koeck et al., 2019, 2020).

Memory retention for long periods may be energetically costly especially when the memory is not used (Fernö et al., 2020), as risk-averse behavior conflicts with foraging or mating activities, even in the absence of a threat (Kraemer and Golding, 1997; Killen and Brown, 2006; Ferrari et al., 2010). In rapidly changing environments, adaptive forgetting frees up memory resources that can be used to learn new behaviors in the current environment (Kraemer and Golding, 1997; Brown et al., 2013). The privately hooked carp reduced hook avoidance due to memory loss to non-significant differences relative to control fish before month 7, perhaps due to unneeded memory caused by the absence of threatening hooks in the preceding months. It is possible that continued fishing creates a constant source of fear, which can reduce memory loss and reduce the general vulnerability of previously captured and other fish as reported by Koeck et al., (2019, 2020) in trout. Further work with more-than-one-time learning are needed to fully examine hook avoidance of carp.

Our research does not support the often-cited (e.g., Sneddon et al., 2003; Braithwaite, 2010) finding by Beukema (1970b) that a one-trial hooking event creates memory retention that lasts more than one year in carp. Learning ability in carp can be strain dependent (Wohlfarth et al., 1975; Suzuki et al., 1978), but even if Beukema's (1970b) carp had better learning abilities than the fish we used in our experiment, Raat's (1985) and our findings suggest that such behavior shall not be generally expected and memory loss can reinstall angling-naïve carp after a few months. Of course, it is possible that differences in experimental set up and continued fishing, rather than truly a one-time-event, could create alternative outcomes.

No aversions to distinct food items were found in the present study, as all treatments ingested freely available food (corn or pellets) in a similar amount when no sham rig was present. This indicates that the observed hook avoidance was not caused by aversion to corn as bait, and only the combination with a sham rig caused the more cautious behavior in carp. Previous work in ponds and lakes has also shown that angled carp do not avoid feeding patches on which angling activity happens (Klefoth et al., 2013; Mehner et al., 2019) and that increased food amounts increase catch rates in carp (Arlinghaus and Mehner, 2003; Žák, 2021), suggesting carp are attracted to angling baits and groundbait even if the patches are fished. This is presumably because the food is of high nutritional quality, of high digestibility and readily available (Niesar et al., 2004; Arlinghaus and Niesar, 2005). Accordingly, carp must have developed visual or other mechanisms to recognize the presence of a hook associated with a bait and use some form of visual or tactile cue during the sorting of bait after the uptake. Indeed, Klefoth et al. (2013) described how carp approached places of recent hooking experiences with a predator inspection behavior and were able to detect angling rigs without being hooked or expelling hooks after pickup, presumably relying most on visual and tactile cues. Evidence that visual cues are involved can also be inferred from the vulnerability to angling increasing in situations with low visibility (at night) (Monk and Arlinghaus, 2017; Žák, 2021). Monk and Arlinghaus (2017) were able to track recently captured carp visiting baited feeding patches in a natural lake without rehooking them, providing further evidence that carp are able to avoid or expel fishing hooks while continuing foraging on free-bait. Moreover, Lovén Wallerius et al. (2020) reported for the same study fish that privately and socially hooked carp were significantly slower in ingesting a free available corn kernel in the presence of a sham rig compared to situations when a corn kernel was presented alone, which is suggestive of carp using visual cues to identify the angling hook. In summary, the collective evidence so far suggests that the fish might approach a bait once visually identified more cautiously and otherwise be able to spit out hooks during the sorting process in the mouth, as shown by Klefoth et al. (2013) in video recordings. We conclude that the hook avoidance behavior of carp has less to do with avoiding dangerous patches or bait and more to do with the ability to identify hooks as threatening and either avoid ingestion or improve the ability to spit out hooks with a bait.

5. Conclusions and implications

Our work demonstrates that memory loss reduces privately learned hook avoidance back to control levels by month 7, while maintaining more cautious behaviors towards baited hooks at this time period. We also revealed that a social hooking experience cannot be detected after 7 months or longer. Therefore, our work does not confirm the often-cited findings from Beukema (1970b) that one-trial hooking is sufficient to lead to a sustained drop in angling catchability for over a year in carp. Although hook avoidance may not be sustained over several months, at least temporarily (e.g., a few days) learned hook avoidance will make carp more difficult to catch and might reduce catchability over time (Monk and Arlinghaus, 2017). Altered catchability on the population level due to learning can lead to hyperdepleted catch rates (Alós et al., 2015, 2019). Drops in catch rates will negatively affect angler satisfaction (Birdsong et al., 2021), and management actions such as temporal fishing closures could have a positive effect on angling catches (Koeck et al., 2019, 2020). Thus, in intensively fished carp populations, temporary declines in catches may be unavoidable unless one controls

Table A1
Chi-squared tests comparing the aversion/preference to a food item (first ingested item: corn vs. pellet vs. no food) within the feeding experiment across the treatments in month 7 and 14.

Time period (month)	X^2	df	p-value
7	1.57	4	0.81
14	0.82	4	0.94

Table A2
Generalized linear model (GLM, using a "Poisson" distribution) comparing the number of eaten corn 7 and 14 months among treatments. The "Control" treatment was used as reference level. Asterisks indicate significant differences ($p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***).

	Corn			
Coefficients	Estimate	SE	Z-value	*p*-value
7 months				
(Intercept)	0.67	0.78	0.86	0.39
Private	- 0.12	0.22	-0.54	0.59
Social	- 0.08	0.21	- 0.37	0.71
Total length	0.01	0.05	0.29	0.77
14 months				
(Intercept)	- 0.23	0.75	- 0.31	0.76
Private	0.14	0.23	0.63	0.53
Social	0.02	0.22	0.10	0.92
Total length	0.04	0.03	1.30	0.19

Table A3
Generalized linear model (GLM, using a "Poisson" distribution) comparing the number of eaten pellets 7 and 14 months among treatments. The "Control" treatment was used as reference level. Asterisks indicate significant differences ($p < 0.05$ *; $p < 0.01$ **; $p < 0.001$ ***).

	Pellet			
Coefficients	Estimate	SE	Z-value	*p*-value
7 months				
(Intercept)	0.38	0.81	0.47	0.64
Private	0.01	0.22	0.04	0.97
Social	- 0.28	0.22	- 1.28	0.20
Total length	0.03	0.05	0.59	0.55
14 months				
(Intercept)	- 0.02	0.77	- 0.02	0.98
Private	0.24	0.22	1.08	0.28
Social	< - 0.01	0.23	- 0.02	0.99
Total length	0.03	0.03	0.95	0.34

fishing effort for a few months, after which carp can again become catchable to the same rates as angling-naïve fish. However, the sustained lower vulnerability (as indicated by the speed to pick up baits) still shown by private fish at month 7 suggests that recovery of naïve behavior towards angling hooks may take several months in carp populations. The extent to which alterations of vulnerability to fishing is present in other species and with other fishing gears is worthy of further study.

CRediT authorship contribution statement

PC, MLW, RA conceptualization of the study, PC data generation, PC, MLW, CTM, RA, data analysis, PC, CTM, SJC, RA interpretation of the results, PC and RA wrote the paper, with edits from the other co-authors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix

(See Appendix Tables A1-A3).

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