Angling-induced hook avoidance and the importance of social learning

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Abstract

It is well known that fish become difficult to catch after experiencing a catch-and-release event (i.e. captured and released back to the water). When catch rates decline in catch-and-release fisheries despite constant fish densities, the intuitive explanation is that fish learn to avoid baits as a result of the unpleasant experience of being hooked. Studies on fish cognition have, however, revealed that information transmitted between individuals is often involved in shaping behaviours. The focus of this study was therefore to determine whether social information use affects the hook avoidance response following catch-and-release. To investigate this, hatchery reared rainbow trout were subjected to different levels of angling exposure and subsequently targeted by anglers. The results suggest that private experience explains most of the avoidance tendency, but a close to significant effect of social angling exposure indicates that socially acquired information may be influencing the learning process.
Introduction

Transfer of information between individuals is referred to as social learning. Learning through social interactions has attracted interest primarily from two different research fields. Psychologists typically look at animals’ ability to imitate behaviours and compare their mental processes to those of humans. Behavioural ecologists on the other hand generally focus on how behaviours can be adopted and altered through social learning and possible fitness effects related to such changes (Heyes, 1994). Intuitively, the ability to imitate the behaviour of another individual seems cognitively demanding and researchers have accordingly directed their efforts primarily towards mammals, like primates (Whiten, 2011) and rodents (Galef & Giraldeau, 2001). The cognitive capabilities of other animal taxa were simply considered insufficient for social learning to have any considerable influence on their behaviour (Laland, Brown, & Krause, 2003). During the last decades, however, this notion has increasingly been challenged. Social information transmission has now been demonstrated in numerous non-mammal species (Danchin, 2004). Fish are relatively well studied and many species are now known to utilize information acquired from observing conspecifics, to increase their performance in various situations and contexts (Brown & Laland, 2003).

Social learning has an obvious advantage to individual learning when it comes to risk avoidance. If a naïve individual can learn to identify a threat by observing the behaviour of experienced individuals, it will have a better chance of responding adequately when faced with a similar threat. To acquire such knowledge through personal learning, the individual would have to expose itself directly to the threat (Mathis, Chivers, Jan, & Smith, 1996). Learning through social interactions can, in addition, be a time and energy efficient way of acquiring information about the environment, in comparison to the trial-and-error method (Laland et al., 2003). From a fitness perspective, however, the rapid transmission of information is not beneficial per se. If naïve fish are unable to discriminate between naïve and experienced demonstrators, maladaptive behaviours can spread quickly among observers, given that they rely on social rather than private information. Acquisition of social information may also constrain the ability of an
individual to collect private information (Giraldeau, Valone, & Templeton, 2002).

Social learning is not necessarily restricted to imitation of observed behaviours. Certain chemicals that are released from the epidermis of fish when being attacked by a predator, are known to function as alarm signals (Chivers & Smith, 1998). Development of associations between the chemical cues and the initially neutral predator cues, leading to predator avoidance also in absence of the alarm chemical, can be viewed as a form of social learning. The importance of visual and chemical social cues, in antipredator behaviour, have been reported by many studies (Griffin, 2004).

In recreational fishing, catch-and-release angling (i.e. releasing fish back to the water following capture and unhooking) has become a wide-spread practice. Mandatory or recommended size and bag limits and strictly “no-kill” regulations are used to maintain viable populations despite strong angling pressure (Cooke & Schramm, 2007). In addition, voluntary releases during recreational angling are common and an estimated 30 billion individuals are released globally each year (Cooke & Cowx, 2004). Discarded and released fish are often ignored in fisheries statistics. Mortality due to hooking, handling, air exposure etc. typically ranges between 15 and 30%. Depending on the angling pressure, neglecting this effect could have serious consequences for stock assessments and population management (Muoneke & Childress, 1994). Interspecific variation in post-release mortality are however large, and factors like hooking position and water temperature affects the survival probability of released fish (Bartholomew & Bohnsack, 2005). In addition to hooking mortality, stress induced physiological and behavioural changes caused by hooking, handling, air exposure and exhaustion have been observed in a number of frequently targeted fish species (e.g. Cooke, Philipp, Dunmall, & Schreer, 2001; Halttunen et al., 2010; Klefoth, Kobler, & Arlinghaus, 2008; Philipp, Toline, Kubacki, Philipp, & Phelan, 1997; Schreer, Resch, Gately, & Cooke, 2005).

In commercial fisheries, size-selective harvesting has been shown to affect life history traits, like age and size at sexual maturation, in exploited populations of cod (Gadus Morhua) (Olsen et al., 2004) and Chinook salmon (Onchorhyncus tshawytscha) (Kinnison, Quinn, Unwin, & Unwin, 2011). In recreational fisheries, behavioural traits like wariness, boldness, aggressiveness and activity are likely to be affected by selection
The strength of angling-induced selection depends on trait heritability, the fitness differential between alternative phenotypes and the overall angling pressure (Kuparinen & Merilä, 2007). In catch and release fisheries, post-release survival rates and any physiological and/or behavioural impairments resulting from the catch event, should also be considered.

Moreover, if learning capacity differs between individuals, certain individuals might be more vulnerable to repeated captures. Poor learners would have reduced chances of long term survival if subjected to multiple catch-and-release events. Evidence for behavioural syndromes – consistent behavioural differences between individuals – have been presented for a number of fish species, like stickleback (Gasterosteus aculeatus) (Huntingford, 1976), pumpkinseed sunfish (Lepomis gibbosus) (Wilson, Coleman, Clark, & Biederman, 1993), brown trout (Salmo trutta) (Höjesjö et al., 2011) and rainbow trout (Onchorhyncus mykiss) (Wilson & Stevens, 2005). Some attempts have successfully linked inter-individual behavioural variation with learning capacity (Askey, Richards, Post, & Parkinson, 2006). Activity, aggressiveness, boldness and exploration tendency (collectively referred to as temperament) are often positively correlated traits (Sih, Bell, Johnson, & Ziemba, 2004; Sneddon, 2003). The learning capacities of highly active and bold individuals are generally lower than for those that are less active and bold (Sih, Bell, & Johnson, 2004) but the opposite relationship was found in Panamanian bishop fish (Brachyrhaphis episcopi) (DePasquale, Wagner, Archard, Ferguson, & Braithwaite, 2014).

The intrinsic vulnerability to angling (i.e. the propensity to take the angler’s bait or lure) also differs between individuals (Garrett, 2002). Recent findings suggest that such variance can be related to the previously mentioned temperament continuum. Again, fish at the active/aggressive/bold side of the scale seem to be more vulnerable (Biro & Post, 2008; Härkönen, Hyvärinen, Niemelä, & Vainikka, 2016). Angling could consequently drive the distribution of phenotypes towards a higher proportion of “shy” individuals in recreational fisheries. The awareness of the problems related to ecological impacts of catch and release as a management strategy, is increasing. Much effort is directed towards improving the knowledge of direct effects of catch and release on physiology, behaviour, learning and mortality as well as angling-induced evolution.
However, the potential importance of social learning in the context of catch-and-release remains largely unexplored.

In this study, I used hatchery reared rainbow trout (*Onchorhyncus mykiss*) in a semi-natural experimental environment, to investigate the importance of socially transmitted information (exposure to other fish subjected to catch-and-release) in relation to private experience of being caught. I am also interested in how individual catchability variation relates to social and private experiences of catch-and-release. If behavioural responses or learning capability varies between behavioural types, such information potentially reflects temperament-driven vulnerability to catch-and-release.

Based on the documented learning capacities and the intraspecific temperament differences found in fishes, I hypothesize that: i) Private (direct) experience of catch-and-release, in addition to social (indirect) experience of conspecifics being caught and released, will reduce the catchability to a higher degree than social experience alone. ii) Disturbance caused by the angling will reduce the catchability relative to undisturbed fish, but not to the same extent as social experience of catch-and-release. iii) Active, presumably aggressive and risk-prone individuals are less capable of acquiring information socially, and therefore more vulnerable to angling.

**Methods**

**Experimental setup**

The experiments were conducted in the facilities of the Swedish Anglers’ association (Sportfiskarna) at Sjölyckan, located in the eastern parts of Gothenburg, Sweden (57°41'36.1"N 12°2'11.8"E). Three consecutive rounds of the experiment were carried out between 8 September and 5 November 2016.

The experimental system consisted of four stone-wall dams measuring 30x24 meters. The depth was approximately 2 meters. Inflow from nearby Lake Delsjön and outflow was regulated through a valve system. Prior to the experiment, the ponds were drained and cleaned from macrophytes and debris. To minimize differences in feeding
motivation, caused by potential differences in the ability to acquire food, between e.g. shy and bold individuals (Cutts, Betcalfe, & Caylor, 1998), no food was provided during the experiment. Limited amounts of invertebrates such as bivalvia and trichoptera were, however, present in the ponds.

In order to measure individual fish activity, four radio-frequency identification antennas (RFID) were deployed in each pond (see figure 1 for approximate positions). The antennas consisted of a triple-looped copper wire inside a PVC-pipe, forming vertically erected rectangles (2.2 x 2.3 m; L x H), spanning the water column. Wooden sticks were used to secure the antennas to leca blocks buried in the substrate. A tuning capacitor and a half-duplex RFID-reader (Oregon RFID, Portland, Oregon) was connected to each antenna.

Figure 1. Schematic figure of an experimental pond. Lines denote the approximate positions of the four radio-frequency antennas.

Prior to each round, hatchery reared rainbow trout (*Onchorhyncus mykiss*; Mean ± s.d: Mass = 391.6 ± 55.1 g; Fork length = 31.6 ± 1.5 cm) were transported from Källefall Hatchery (58°10’12.3”N 14°4’47.6”E) to Sjölyckan and placed in plastic holding tanks (2 x 2 x 0.5 m; L x H x D). After approximately one hour of acclimation, 163 fish per replicate were anaesthetized with tricaine mesylate (round 1 and 3; 150 mg l⁻¹) buffered with NaHCO₃ (300 mg l⁻¹) or benzocaine (round 2; 400 mg l⁻¹), photographed, measured for mass and fork length and tagged with passive integrated transponders, PIT (23 x 3.65
mm, 0.6 g, Texas Instruments, Dallas, Texas) to enable individual identification and activity scoring. PIT-tags were inserted into the abdominal cavity through a small incision with antiseptic cream applied to the wound.

A subset of 30 individuals each in replicate 1 and 3 had heart rate loggers (HRL; DST milli-HRT, Star-Oddi) implanted to enable monitoring of heart rate throughout different phases of the experiment. Heart rate loggers were inserted through an approximately 30 mm incision along the midventral line, between the pelvic and pectoral fins. During the surgical procedure, tricaine mesylate (75 mg l⁻¹) buffered with NaCHO₃ (150 mg l⁻¹) was pumped across the gills to keep the fish anaesthetized. Loggers were positioned longitudinally in the abdominal cavity and incisions were sutured and smeared with antiseptic cream. An additional subset of 10 individuals each in replicate 1 & 3 were used as “shams” i.e. they underwent identical surgical treatment, but no loggers were implanted. Heart rate variation falls outside the scope of the current analysis but will be addressed in a future study.

Following tagging/surgery, fish were placed in a recovery tank (1.0 x 1.0 m) for observation. When the fish had resumed normal swimming and respiratory motion, they were distributed among the four experimental ponds and left to acclimate for 8 days before treatment (fig 2). In addition to the 163 fish released in the experimental ponds, approximately 30 additional fish per round were released in an additional pond (pond 5). Here, the fish where stocked together with larger rainbow trout that remained in the pond since previous releases by the Anglers’ association. Fish from pond 5 were subsequently used for catch-and-release exposure during pre-treatment (see Pre-treatments). These individuals were not used in any analysis, hence possible catchability effects caused by differential food intake was not a concern. The fish in pond 5 were therefore provided with food pellets. Pond 5 was not emptied between experimental rounds, hence fish from the first round was kept in the pond for the entire experimental period.

Individual activity was monitored in one pond at a time for 24 hours. The monitoring periods were repeated four times per pond during each replicate of the experiment (figure 2). In each pond, monitoring was conducted before (2 periods), during or after
pre-treatment (1 period) and during angling (1 period), hence activity levels could potentially have been affected by pre-treatments and angling. No such effects where, however, found in a recent study in which identical RFID-equipment and similar treatments were used (Koeck et al. in revision). Detection data from all monitoring periods were therefore pooled in the analysis. Whenever a fish came within the detection range of an antenna (approximately 50 cm from the surface area of the frame) the individual’s PIT-tag was registered together with the time and date of the detection.

**Pre-treatments**

Fish were randomly assigned to four groups that were stocked in separate ponds and exposed to different treatments. In each round, all treatments were conducted simultaneously during one hour per day on three consecutive days (figure 2). To control for possible pond-specific effects, the treatment order was changed between rounds so that no treatment was repeated within the same pond. The time of the angling exposure was adjusted between rounds to account for seasonal changes in light conditions, so that each angling exposure ended approximately one hour before sunset.

In the *private exposure treatment*, two anglers, placed on each short side of the pond, used passive fishing gear – spinning rod, floater, sinker and barbless hook baited with shrimp, for 60 minutes of angling. Anglers chose freely were to cast, how long to keep the bait at one spot and the depth at which the bait was presented. When a fish was caught, knotless landing nets were used to transfer the fish to a water-filled plastic bucket in which it was unhooked and identified with a handheld PIT-reader. During the remainder of the angling event the caught fish were kept in recovery tanks. Immediately after the angling event, all caught fish were transferred back to their respective pond, hence a fish could only be caught once in each angling event but potentially up to three times during the three days of treatment. Deep-hooked fish were euthanized with a sharp blow to the head.

In the *social exposure treatment*, each event began with an angler catching one fish, using identical angling gear as in the private exposure treatment, except for a barbed hook to reduce the risk of loosing hooked fish. When the first fish was caught and identified by
its PIT-tag number it was not released back to the same pond, instead it was transferred to the non-experimental pond (pond 5). No more individuals were caught in the experimental pond during the social exposure angling. Non-focal fish however, were caught in pond 5 and transferred to the treatment pond where they were displayed for approximately 30 seconds, while connected to the anglers line. After the exposure, the fish were landed using a knotless rubber net and transferred back to pond 5. The number of displayed individuals (including the first catch) was kept equal to the number of individuals caught in the simultaneously conducted private exposure treatment. The purpose of this procedure was to expose observers to a similar level of disturbance/opportunity to acquire information, as experienced indirectly by individuals in the private exposure treatment, without providing any focal fish with private experience of catch-and-release. The difference in initial sample size between the social exposure and the other treatments (43 compared to 40 per replicate) was set to compensate for the removal of one individual per exposure angling, theoretically resulting in equal post-treatment sample sizes. In both the first and the second round of the experiment, one non-focal individual was lost during exposure. These individuals remained in the ponds until the subsequent angling events, during which they were caught and removed.

An angling disturbance treatment was included in the experimental design to account for the possible effects of disturbance related to the angling method itself i.e. disturbance caused by casting and retrieving the tackle, the anglers´ movements etc. The “angling” was performed in the same way as in the private exposure treatment but no bait or hooks were used.

No angling was conducted in the control treatment. The only potential disturbance the fish were exposed to was from people walking along the sides of the dam.

Angling

48 hours after the last day of pre-treatment, standardized angling was conducted simultaneously in all four experimental ponds during four consecutive days (figure 2). The duration of each angling event was one hour of effective angling. Eight anglers were
deployed, with one angler positioned on each short side of the dams. Every tenth minute their position was changed to control for differences in fishing technique/skills. As in the private exposure treatment, barbless hooks baited with shrimps were used. Caught fish were kept in recovery tanks during the remainder of the angling event and, after identification, released back to their respective ponds. Each individual could thus potentially be caught up to four times. The angling events ended approximately one hour before sunset.

When one round of angling was complete, the ponds were drained and the fish were collected for measurements of individual mass and fork length. The ponds were refilled before the start of the next round. After 2-3 days in recovery tanks, remaining rainbow trout were released in one of the anglers’ association’s nearby lakes.

**Experimental round**

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**Figure 2.** Order and duration of the different parts of a 16-day experimental round. Monitoring 1-4 refers to four periods of activity monitoring. Each pond was monitored for approximately 24 hours per period.

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**Data handling and statistical analysis**

Individual activity estimates were based on the cumulated number of detections over the monitoring periods, divided by number of monitoring days. To control for inflated estimates due to repeated detections of individuals residing in the vicinity of one
particular antenna, multiple detections close to each other in time (within 6.84 seconds), at one single antennae, were discarded.

Individual body condition was calculated as Fulton’s condition factor (K): $m_f/FL^3$, with $m_f$ = mass at the beginning of the experiment and $FL$ = fork length at the beginning of the experiment. Individual growth rate during the experimental period was calculated as specific growth rate (SGR) according to the formula: $(\ln(m_f) - \ln(m_i)) / t \times 100$, with $m_f$ = mass at the beginning of the experiment, $m_i$ = mass at the end of the experiment and $t$ = the duration of the experiment (in days). Two individuals were excluded from analysis of Fulton index and growth in fork length, due to unrealistic growth values (3.3 and 3.0 cm growth) probably resulting from measurement errors.

A Cox proportional hazard regression (“coxph” function, “survival” package, R) was used to evaluate possible associations between treatment and catchability i.e. to what degree the pre-treatments affected the chances of an individual being caught. To explore relationships between vulnerability to angling and individual differences in activity and initial mass, these measurements were included in the initial Cox proportional hazard regression. Initial mass was considered a more reliable measure of fish size than fork length, since many fish showed caudal fin deformities. One-way analysis of variance were conducted to investigate possible between-group variation in activity and initial mass. Both activity and and initial mass were, however, excluded from the model due to non-significant effects on catchability (table S1 in supplementary material).

Experimental round was included in the model to account for potential catch rate differences between the three rounds. There were non-significant interactions between rounds and treatments, indicating similar treatment effects across all three rounds of the experiment. The interaction terms were thus excluded from the model. The reduced model showed that the catch rate was significantly lower in round 3, relative to round 1 (table 2). Although this difference seemed to reflect a general catch decrease rather than being related to any specific treatment, experimental round was responsible for a considerable fraction of the explained variance ($r^2_{Cox (treatment + round)} = 18.2\%$; $r^2_{Cox (treatment)} = 14.3\%$), and was therefore kept in the model. Treatment and experimental round were thus included in the final Cox proportional hazard model.
The model accounted for only one event per individual, i.e. the response variable was the time until first catch. Repeated catches were thus excluded from the analysis. The control treatment and round 1 were used as reference levels in the model. All statistical analysis were performed using R, version 3.3.3.

Unfortunately, the final sample sizes for several groups deviated from the intended 40 individuals per treatment and replicate. The initial idea was to have subsets of 10 HRL-implanted individuals/shams per treatment in each round. During the first round however, a large proportion of the HRL-implanted fish had severely infected incision wounds. High water temperature, facilitating bacterial growth, was believed to underlie the infections. All HRL-fish and shams from the first round were therefore discarded from analysis and no HRL-fish were used in round 2. Heart rate loggers were, however, used again in round 3, when water temperatures had decreased. These individuals did not show signs of infections and were thus included in the analysis. One HRL-implanted individual in the social exposure treatment was found dead before the start of the treatment and was replaced by a non-implant individual. Furthermore, not all individuals in the private exposure treatment were caught during the exposure angling. Since uncaught individuals lacked private experience of catch-and-release, they were discarded from the main analysis (but see table supplementary material for an alternative analysis including all individuals).

Results

In total, 79.8% of the focal fish were caught at least once during the angling events (N=411). The largest proportion of fish were caught in round 2 (0.87), followed by round 1 (0.84) and 3 (0.69)(table 1, figure 2). Regarding the treatments, the largest proportion were caught in the control treatment (0.93), followed by disturbance (0.87), social exposure (0.81) and private exposure (0.49) (table 1, figure 2).

Fulton’s condition factor (K) at the beginning of the experiment averaged 1.24 (SD = ±0.076). In general, the fish showed a decrease in mass during the experiment
(mean = -15.39 g; SD = ±11.05 g), hence negative specific grow rates (mean = -0.22; SD ±0.17) whereas the average change in fork length was slightly positive (mean = 0.21 cm; SD ±0.27 cm).

Table 1. Proportion of individuals caught per replicate and treatment. Numbers inside parentheses represent sample size for each group.

<table>
<thead>
<tr>
<th>Replicate</th>
<th>Control</th>
<th>Disturbance</th>
<th>Social Exp.</th>
<th>Private Exp.</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>1.00 (30)</td>
<td>0.93 (30)</td>
<td>0.84 (32)</td>
<td>0.42 (19)</td>
<td>0.84 (111)</td>
</tr>
<tr>
<td>R2</td>
<td>0.95 (40)</td>
<td>0.95 (40)</td>
<td>0.93 (40)</td>
<td>0.61 (31)</td>
<td>0.87 (151)</td>
</tr>
<tr>
<td>R3</td>
<td>0.85 (40)</td>
<td>0.75 (40)</td>
<td>0.68 (40)</td>
<td>0.41 (29)</td>
<td>0.69 (149)</td>
</tr>
<tr>
<td>Totals</td>
<td>0.93 (110)</td>
<td>0.87 (110)</td>
<td>0.81 (112)</td>
<td>0.49 (79)</td>
<td>0.80 (411)</td>
</tr>
</tbody>
</table>

Figure 2. Proportion fish caught during angling events, per round and treatment.

No significant differences in activity or initial mass were found between rounds (one-way ANOVA; activity: F_{2,408} = 0.87, P=0.42; initial mass: F_{2,408} = 0.97, P=0.38; figure S2 in supplementary material) or pre-treatments (one-way ANOVA; activity: F_{3,407} = 0.80, P=0.49; initial mass: F_{3,407} = 1.16, P=0.33; figure S3 in supplementary material). Neither activity or initial mass had any significant effects on catchability (table S1, figure S4 in
supplementary material).

**Effects of private and social catch-and-release exposure**

The time until first catch was significantly longer for individuals in the private exposure treatment (table 2, figure 3) compared to the control. Private experience of catch-and-release reduced the catchability by 73.3%. Individuals in the social exposure treatment also tended to remain uncaught longer than individuals in the control treatment - the time to first catch was increased with an estimated 23.8% for individuals that were socially exposed to catch-and-release. This relationship however, falls just short of statistical significance ($P=0.061$). No difference in catchability was observed between the disturbance angling and the control treatment (table 2; figure 3).

**Table 2.** Cox-proportional hazard regression, estimating the effect of treatment and experimental round on the time individuals remained uncaught during the angling periods. Control treatment and round 1 were used as reference levels. The number of events refers to the total number of caught fish.

<table>
<thead>
<tr>
<th></th>
<th>$\beta$</th>
<th>$e^{\beta}$</th>
<th>$se(\beta)$</th>
<th>$z$</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disturbance</td>
<td>-0.0887</td>
<td>0.9151</td>
<td>0.1423</td>
<td>-0.623</td>
<td>0.533</td>
</tr>
<tr>
<td>Social Exp.</td>
<td>-0.2721</td>
<td>0.7618</td>
<td>0.1450</td>
<td>-1.877</td>
<td>0.061</td>
</tr>
<tr>
<td>Private Exp.</td>
<td>-1.3192</td>
<td>0.2674</td>
<td>0.1909</td>
<td>-6.910</td>
<td>0.00003</td>
</tr>
<tr>
<td>Round 2</td>
<td>0.2249</td>
<td>1.2522</td>
<td>0.1362</td>
<td>1.651</td>
<td>0.099</td>
</tr>
<tr>
<td>Round 3</td>
<td>-0.3522</td>
<td>0.7031</td>
<td>0.1441</td>
<td>-2.445</td>
<td>0.014</td>
</tr>
</tbody>
</table>

$n=411$, number of events= 327  
Likelihood ratio test= 82.7 on 5 df,  $p=2.22e-16$
Figure 3. Survival curves based on the Cox proportional hazard regression model, illustrating the remaining proportions of uncaught individuals, from day to day, for the four pre-treatments. Red crosses denote the proportion of individuals that remained uncaught throughout the entire angling period.

Discussion

The main focus of the current study was to investigate whether learned hook avoidance are solely due to private catch-and-release experience or if the process is influenced by social information use. Based on the findings, it cannot be concluded that socially acquired information is crucial to the learning process, but the tendency for fish in the social exposure treatment to remain uncaught longer than fish in the control treatment, strongly indicates that social learning contributes to angling-induced hook avoidance.

In line with other studies on catchability, the results clearly show that individuals become harder to catch when subjected to catch-and-release angling. Even though there has not been any direct attempts to partition the underlying mechanism for learned hook avoidance into social and private information use, some demonstrated links between certain tactile and visual cues and increased hook avoidance are suggestive of private learning. For example, common carps (Cyprinus carpio) were able to avoid getting hooked after ingesting baits, presumably do to tactile cues that caused the carps to expel the bait (Klefoth, Pieterek, & Arlinghaus, 2013). The possibility that the rainbow trout used in the private exposure treatment developed similar abilities cannot be
excluded. These fish, unlike fish in the other treatments, were repeatedly exposed to baited hooks and could potentially have learned to avoid them even if they had no private experience a catch-and-release (i.e. were among the fish that were not caught during treatment). It has also been shown that fish learn to avoid conspicuous, artificial baits quicker than natural baits, after catch-and-release (Beukemaj, 1970). The most likely explanation for these findings is that private learning is facilitated by the distinct differences between artificial baits and natural preys. Furthermore, reduced catch rates with increasing angling pressure have been documented for solitary predators like pike (*Esox lucius*) (Kuparinen, Klefoth, & Arlinghaus, 2010) and large-mouth bass (*Micropterus salmoides*) (Anderson & LeRoy Heman, 1969) in catch-and-release fisheries. Considering the limited opportunities for transmission of social information among solitary species, such declines are in themselves indications of private learning. Typically, however, it is not possible to discriminate between social and private learning when angling induced hook avoidance is observed, since catchability experiments designed for other purposes generally allow both ways of information acquisition.

The angling disturbance treatment had little effect on catch rates, indicating that the catchability decreases observed in the private and social angling exposure are not related to a general stress response - caused by the angling method itself. It could be argued that the angling disturbance treatment likely caused less disturbance to the fish than private and social angling exposure since these individuals were not exposed to any hooked fish. If so, differences in hook avoidance between treatments could potentially reflect different levels of stress impact rather than any form of learning processes. Although physiological stress responses in rainbow trout can affect feeding behaviour (Gregory & Wood, 2015), they are typically short-lasting. Plasma concentrations of cortisol, for example, generally return to normal levels within a few hours following an acute stress response (Ruane, Wendelaar Bonga, & Balm, 1999). Thus, it is not likely that the observed differences in catchability are linked directly to elevated cortisol levels, but stress-induced effects on behavioural performance may extend beyond physiological recovery (Schreck, 2000).

Angling disturbance could potentially have affected the fish’s use of space within the ponds. In laboratory environment, common carp have been shown to avoid fishing
locations during angling (Klefoth, Skov, Krause, & Arlinghaus, 2012) However, due to the limited size of the experimental ponds used in the current experiment, the entire pond area was within casting range of the anglers. Hence, even if the fish kept away from the immediate vicinity of the anglers, their encounter rates with the hooks would not be greatly affected.

Significantly fewer fish were caught in round 3 compared to round 1 and 2. This might be an effect of decreased water temperatures and/or shorter activity periods. However, fish activity, as measured by PIT-tag recordings, was not significantly lower in round three than in round 1 and 2. It is also possible that the anglers’ ability to handle the angling gear and the fish was affected by the cold weather.

The hypothesised relationship between behavioural variation and initial vulnerability to angling was not supported by the results. Activity has been shown to correlate with catchability in (Alós, Palmer, & Arlinghaus, 2012; G. P. Garrett, 2002; Thomas Klefoth et al., 2012) and the possibility that more accurate activity estimates than those provided by the RFID-system could have revealed such a link, cannot be excluded. Empirical evidence for increased angling vulnerability among active fish is, however, scarce and the opposite relationship has also been found (Binder et al., 2012). According to pace of life syndrome theory activity, boldness and aggressiveness are expected to be correlated traits (Huntingford, 1976; Sneddon, 2003; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004). Such traits are related to high positions in social hierarchies (Schjolden, Stokshus, & Winberg, 2015; Sundström et al., 2004) which are formed in populations of salmonids when resources are limited (Chapman, 1966). Furthermore, hierarchical rank is related also to body size, with larger fish being more dominant (Johnsson, Nobbelin, & Bohlin, 1999). This is consistent with the temperament continuum, considering that bold and dominant individuals may acquire more food as a consequence of their risk-prone behavioural style (Cutts, Betcalfe & Caylor, 1998; Sundström et al., 2004). In this study initial size did not seem to affect catchability. However, if we assume that small and less active subordinates were prevented to take the bait by large and active individuals, such tendencies could only be expected during the beginning of the angling events, considering that catch rates quickly decreased i.e. there is no point defending a resource when it is no longer desired.
Bold phenotypes can be favoured by selection in hatchery environments (Berejikian, 1995; Johnsson & Abrahams, 1991) and the rainbow trout used in the present study have many generations of hatchery ancestry. Variation in boldness might therefore be higher in natural populations. Thus, the fact that we did not find any correlation between individual traits and catchability does not mean that such relationships cannot exist in natural populations. Furthermore, if the relative importance of private learning, compared to social learning, is higher for bolder individuals (Kurvers et al., 2010), the importance of social learning could be higher for wild populations than indicated by the results, since hatchery reared and presumably bolder fish were used in the experiment. On the other hand, the limited space and lack of complexity in the experimental environment could have facilitated visual contact between individuals. When a fish took the bait, this “mistake” and the following events were likely witnessed by many conspecifics, providing enhanced opportunities for social learning.

In addition to the direct experience of being hooked, fish in the private exposure treatment were surrounded by other fish with private experience of catch-and-release. How the presence of such experienced “demonstrators” could have affected the results is difficult to say, but would be interesting to address in future research. In terms of experimental design, the difficulties to extract the effect of social learning from the total learning effect are challenging, but nevertheless essential to address in future research. Ideally, observers should be exposed to each step of a catch-and-release event – from sensory perception of the bait to post-release behaviour.

Clearly, the use of social information can vary between individuals and between different environmental conditions. My main objective was, however, not to quantify the extent to which rainbow trout rely on social information when making a decision to take the bait or not, but to investigate whether social learning is an actual component of the acquired avoidance behaviour.

In Sweden, rainbow trout have been reared in hatcheries and released in numerous put and take fisheries for many decades (Stanković, Crivelli, Snoj, Stankovi, & Snoj, 2017). Since rainbow trout rarely reproduce naturally in Sweden (Landergren, 1999) constant
input of fish is required to maintain satisfactory densities. Individuals with a high initial vulnerability to angling are at greater risk of getting caught shortly after release compared to less vulnerable fish (Garrett, 2002). In catch-and-kill fisheries, the proportion of cautious fish will thus increase over time. The catch per angling effort will then decrease, even if fish densities are kept constant. A similar decrease is expected also in catch-and-release fisheries, where highly vulnerable individuals are caught quickly and thereafter become reluctant to take a bait again (Askey et al., 2006). Even though social information use is not necessary for fisheries to evolve in such direction, it could affect the speed and strength of this tendency. With high fish densities, less angling pressure would be needed to induce a wide-spread hook avoidance, assuming that social information is involved in the learning process.

From a national ecological perspective, the learning processes of hatchery reared Swedish rainbow trout - incapable of reproducing and predominantly used in put-and-take fisheries, might not seem very important. Globally however, rainbow trout is one of the most widely introduced and frequently targeted species (Stanković et al., 2017). If management efforts can reduce the opportunities for social learning, like increasing structural complexity and thereby restricting the visual contact between individuals, catch rates could be sustained with lower fish densities. Furthermore, population size estimates based on catch-and-release data is likely to underestimate true population sizes, particularly due to private learning but possibly also if hook avoidance behaviour spreads through social learning.

In a broader context, species-specific characteristics need to be taken into account, to investigate relationships between social learning and catch-and-release angling. For example, a condition for learning through intraspecific interactions, would be frequent encounters with conspecifics. Hatchery reared fish and species forming shoals are constantly within eyesight of numerous potential demonstrators. Social species may, in addition, have developed refined abilities to acquire and process social information in response to natural selection (Laland & Williams, 1997).

In conclusion, the results presented in the current study are not decisive evidence that socially transmitted information is involved when rainbow trout develop aversions
towards presented bait, after being caught and subsequently released back to the water. The trend towards decreased catchability in response to catch-and-release exposure though, is a strong indicator of social learning. The hypothesised relationship between individual temperament and catchability was not supported by the results. Future research on learning processes in fish will have to tell if these results are representative also for wild rainbow trout or even other targeted angling species. Given the complexity of learning processes and the circumstances potentially affecting the importance of private and social information, such proceedings will however, require sophisticated angling experiments.

Acknowledgements

I would like to thank Professor Jörgen Johnsson for giving me much needed guidance and valuable feedback throughout the writing of this thesis. I would also like to thank my co-supervisors Dr. Barbara Koeck and PhD student Magnus Lovén Wallerius for their dedicated work and for taking the time to teach me about all aspects of the project. I want to thank the Swedish Anglers´ Association (Sportfiskarna) for all their help and for letting us use their facilities. And finally, thanks to all the anglers for voluntarily participating in the angling events despite the sometimes horrible weather conditions.

References


**Supplementary material**

**Sample size variation**

Replicate 1

**Private exposure treatment**

- 40 individuals at the start.
- 10 HRL-fish were discarded.
- 5 individuals were euthanized during treatment.
- 7 individuals were not caught in the private exposure treatment, hence excluded from main analysis (but see the alternative analysis in supplementary material).
- One HRL-fish was found dead in the private exposure treatment and replaced with a non-logger fish. The non-logger fish was included in the analysis.
- Final sample size: $40 - 10 - 5 - 7 + 1 = 19$

**Social exposure treatment**

- 43 individuals at the start.
- 10 HRL-fish were discarded.
- 3 individuals were supposed to be removed during angling exposure. However, two of the three individuals displayed in the angling exposure were HRL-fish, hence only one of the three additional fish (relative to the other treatments) were removed.
- Final sample size: $43 - 10 - 1 = 32$
**Disturbance angling and control treatment**

- 40 individuals at the start.
- 10 HRL-fish were discarded.
- No additional deviations from the intended sample size.
- Final sample sizes: $40 - 10 = 30$

**Replicate 2**

**Private exposure treatment**

- 40 individuals at the start.
- 1 individual was euthanized during treatment.
- 8 individuals were not caught in the private exposure treatment, hence excluded from main analysis (but see the alternative analysis in supplementary material).
- Final sample size: $40 - 1 - 8 = 31$

**Social exposure, angling disturbance and control treatment**

- No deviations from the intended sample size (n=40).

**Replicate 3**

**Private exposure treatment**

- 40 individuals at the start.
- 1 individual was euthanized during treatment.
- 10 individuals were not caught in the private exposure treatment, hence excluded from main analysis (but see the alternative analysis in supplementary material).
- Final sample size: $40 - 1 - 10 = 29$

**Social exposure, angling disturbance and control treatment**

- No deviations from the intended sample size (n=40)
Cox proportional hazard regression – full model

Table S1. Initial Cox-proportional hazard regression, estimating the effect of treatment, experimental round, initial mass and activity on the time individuals remained uncaught during the angling periods. Control treatment and round 1 was used as reference levels. The number of events refers to the total number of caught fish. Initial mass and activity were excluded in the final model (table 2, figure 4 in main text).

<table>
<thead>
<tr>
<th></th>
<th>β</th>
<th>exp(β)</th>
<th>se(β)</th>
<th>z</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disturbance</td>
<td>-0.078</td>
<td>0.925</td>
<td>0.1423</td>
<td>-0.623</td>
<td>0.582</td>
</tr>
<tr>
<td>Social Exp.</td>
<td>-0.282</td>
<td>0.754</td>
<td>0.1450</td>
<td>-1.877</td>
<td>0.052</td>
</tr>
<tr>
<td>Private Exp.</td>
<td>-1.306</td>
<td>0.271</td>
<td>0.1909</td>
<td>-6.910</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Round 2</td>
<td>0.241</td>
<td>1.272</td>
<td>0.1362</td>
<td>1.651</td>
<td>0.078</td>
</tr>
<tr>
<td>Round 3</td>
<td>-0.340</td>
<td>0.712</td>
<td>0.1441</td>
<td>-2.445</td>
<td>0.018</td>
</tr>
<tr>
<td>Initial mass</td>
<td>0.001</td>
<td>1.001</td>
<td>0.001</td>
<td>0.506</td>
<td>0.613</td>
</tr>
<tr>
<td>Activity</td>
<td>0.000</td>
<td>1.000</td>
<td>0.000</td>
<td>1.342</td>
<td>0.180</td>
</tr>
</tbody>
</table>

n= 411, number of events= 327
Likelihood ratio test= 84.58 on 7 df, p= 1.554e-15

Effects of private and social catch-and-release exposure – alternative analysis

The Cox proportional regression model, in the main text, examining the effects of treatment and round on the time to first catch, did not account for individuals that were not caught during exposure angling in the private treatment. An alternative analysis including these individuals yielded a similar outcome - a highly significant effect of private catch-and-release exposure, a weaker, non-significant effect of social exposure and a significantly reduced catch rate in round 3 (table S2; Figure S1).
Table S2. Cox-proportional hazard regression, estimating the effect of treatment and experimental round on the time individuals remained uncaught during the angling periods. Individuals that were not caught during treatment angling in the private exposure treatment included. Control treatment and round 1 was used as reference levels. The number of events refers to the total number of caught fish.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>β</th>
<th>exp(β)</th>
<th>se(β)</th>
<th>z</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disturbance</td>
<td>-0.0818</td>
<td>0.9215</td>
<td>0.1423</td>
<td>-0.57</td>
<td>0.5656</td>
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<tr>
<td>Social Exp.</td>
<td>-0.2523</td>
<td>0.7770</td>
<td>0.1446</td>
<td>-1.75</td>
<td>0.0809</td>
</tr>
<tr>
<td>Private Exp.</td>
<td>-1.2993</td>
<td>0.2727</td>
<td>0.1721</td>
<td>-7.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Round 2</td>
<td>0.1681</td>
<td>1.1830</td>
<td>0.1328</td>
<td>1.27</td>
<td>0.2055</td>
</tr>
<tr>
<td>Round 3</td>
<td>-0.3961</td>
<td>0.6730</td>
<td>0.1402</td>
<td>-2.83</td>
<td>0.0047</td>
</tr>
</tbody>
</table>

n= 436, number of events= 342
Likelihood ratio test= 96.3 on 5 df, p=0

Figure S1. Survival curves based on the Cox proportional hazard regression model, illustrating the remaining proportions of uncaught individuals, from day to day, for the four pre-treatments. All individuals in the private exposure treatment included. Red crosses denote the proportion of individuals that remained uncaught throughout the entire angling period.
Individual variation in activity and initial mass

Figure S2. Boxplots illustrating the distribution of a) activity scores (number of detections per day) and b) initial mass, per experimental round. The line inside the boxes represent the median, the top of the boxes the higher quartile, the bottom of the boxes the lower quartile and the whiskers represent the maximum resp. minimum values excluding outliers.

Figure S3. Boxplots illustrating the distribution of a) activity scores (number of detections per day) and b) initial mass per treatment. The line inside the boxes represent the median, the top of the boxes the higher quartile, the bottom of the boxes the lower quartile and the whiskers represent the maximum resp. minimum values excluding outliers.
Fig S4. Boxplots illustrating the distribution of a) individual activity scores (number of detections per day) and b) initial mass for rainbow trout remaining uncaught, from angling day 1 to 4. The line in the boxes represent the median, the top of the boxes the higher quartile, the bottom of the boxes the lower quartile and the whiskers represent the maximum resp. minimum values excluding outliers. The numbers inside the boxes shows the number of uncaught individuals for the specific day. Day 1 represents the start of the angling, hence all focal individuals are present. Boxes at day 5 represent individuals that remained uncaught throughout the entire angling period.