ORIGINAL ARTICLE

Socially induced stress and behavioural inhibition in response to angling exposure in rainbow trout

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Abstract

It is well known that fish can learn to avoid angling gear after experiencing a catch-and-release event, that is, after a private hooking experience. However, the possible importance of social information cues and their influence on an individual's vulnerability to angling remains largely unexplored, that is, social experience of a conspecific capture. The effects of private and social experience of hooking on the stress response of fish and subsequent catch rates were examined. Hatchery-reared rainbow trout, *Oncorhynchus mykiss* (Walbaum), were implanted with heart rate loggers and experimentally subjected to private or social experience of hooking. Private and social experience of angling induced an increased heart rate in fish compared with naïve control fish. While private experience of hooking explained most of the reduced vulnerability to capture, no clear evidence was found that social experience of hooking affected angling vulnerability in fish that had never been hooked before. While both private and social experiences of angling constitute significant physiological stressors for rainbow trout, only the private experience reduces an individual's vulnerability to angling and in turn affecting population-level catchability.

KEYWORDS

angling vulnerability, fish behaviour, heart rate, learning, *Oncorhynchus mykiss*, recreational fisheries

1 | INTRODUCTION

Recreational fishing is common in all industrial countries (Arlinghaus, Tillner, & Bork, 2015). In contrast to commercial fisheries, recreational fishing is a leisure activity where only a portion of the catch is kept for nutritional purpose (Cooke & Cowx, 2006; Cooke et al., 2018). Worldwide reports about declining and collapsed fish populations have mainly been attributed to commercial fisheries (Worm et al., 2009). However, increasing attention about recreational fishing and its induced impact on fish population has risen in some countries (Cooke & Cowx, 2004; Lewin, Arlinghaus, & Mehner, 2006; Post et al., 2002). To support angler satisfaction and reduce

the impact of recreational fishing, fisheries managers have implemented harvest regulations and other management strategies, such as stocking (Arlinghaus et al., 2007; FAO, 2012). One approach to deal with the potential of angling-induced overfishing is size-based harvest regulation that involves mandatory catch-and-release (C&R) of undersized fish, and the promotion of voluntary C&R of harvestable fishes where fish are released back to the water following capture and unhooking (Bartholomew & Bohnsack, 2005; Cooke & Schramm, 2007; Policansky, 2002). The concept behind C&R relies on the conservation of fish populations, with the intention to sustain catch rates (Arlinghaus et al., 2007). Achieving these aims demands releasing fish without substantial injuries and other lasting

sublethal physiological and behavioural impacts. Literature reviews have revealed substantial interspecific and contextual variation in post-release impacts and mortality, including hook-related injuries and physiological/behavioural responses to C&R, demanding species-specific research to evaluate the effects of C&R (Arlinghaus et al., 2007; Cooke & Suski, 2005).

In addition to potential lethal impacts, C&R can produce multiple sublethal stress responses, including elevated plasma concentrations of cortisol (Meka & McCormick, 2005; Pankhurst & Dedual, 1994), increased cardiac activity (i.e., heart rate, cardiac output and stroke volume) (Anderson et al., 1998; Cooke, Philipp, Dunmall, & Schreer, 2001; Cooke, Schreer, Dunmall, & Philipp, 2002) and behavioural changes for a certain period following the release (Klefoth, Kobler, & Arlinghaus, 2011;). As a consequence, individual fish can develop hook avoidance behaviour through private experiences of hooking (Askey, Richards, Post, & Parkinson, 2006; Beukema, 1970a, 1970b; Klefoth, Pieterek, & Arlinghaus, 2013; van Poorten & Post, 2005; Raat, 1985; Young & Hayes, 2004). In addition, population-level catchability has been found to be affected by angling effort without necessarily all fish being hooked and released (e.g., ; Kuparinen, Klefoth, & Arlinghaus, 2010; Alós, Palmer, Trías, Díaz-Gil, & Arlinghaus, 2015; Wegener, Schramm, Neal, & Gerard, 2018). Experimental pond studies with carp, *Cyprinus carpio* L. (Beukema, 1970a; Klefoth et al., 2013; Raat, 1985), and pike, *Esox Lucius* L. (Beukema, 1970b), have suggested that social learning might play a role in observed decreases of overall catchability. These studies suggested that physiological and behavioural stress responses from previously caught individuals may also carry over to affect non-hooked conspecifics, eliciting a hook avoidance behaviour in these individuals through a social learning mechanism (Laland, Brown, & Krause, 2003), thereby decreasing the overall catchability of the targeted fish population. The only study directly testing this hypothesis was conducted on largemouth bass, *Micropterus salmoides* (Lacépède) (Wegener et al., 2018), but it failed to find evidence that social learning reduced catchability in this species. However, as social behaviours and the ability to learn differ considerably in freshwater fishes (Coble, Farabee, & Anderson, 1985), the results on largemouth bass by Wegener et al. (2018) may not be generalisable to other species.

Social learning is defined as long-term behavioural changes to a stimuli derived from the interactions with or observations of other individuals, that is, public information use (Mesoudi, Chang, Dall, & Thornton, 2016). Social learning has an obvious adaptive value to private learning in terms of risk avoidance. For example, if an individual can learn to identify a threat by observing the behaviour of experienced individuals without taking the risk itself, it could have an equally good chance of responding adequately when faced with a similar threat (Laland et al., 2003). Social learning is, however, not restricted to observation. For example, chemical cues released from the epidermis of injured fish are known to function as alarm signals (Schreckstoff) that can trigger a response in the receiving fish (Brown & Smith, 1997; Chivers & Smith, 1998). Moreover, by developing associations between alarm chemicals and the aversive response of conspecifics towards an initially neutral predator, an individual may learn to identify the predator and evoke an avoidance response against it, even in the absence of conspecifics or alarm chemicals (Griffin, 2004). It is unknown whether such effects occur in hook-and-line fishing, where the threat cues are mainly related to olfactory and visual stimuli, and whether the experience of observing conspecifics being hooked and released will affect physiological responses and cause behavioural changes (Meekan, McCormick, Simpson, Chivers, & Ferrari, 2018).

The aim of the present study was to evaluate the effect of angling experience and its impact on catch rate and heart rate—used as a proxy to measure stress response (Wendelaar Bonga, 1997)—by exposing rainbow trout, *Oncorhynchus mykiss* (Walbaum), in ponds to different levels of angling exposure, followed by catch-and-release angling. Based on the documented learning capacities of fish, as well as the known physiological and behavioural stress responses of previously hooked fish, the following hypotheses were tested: (a) social experience of C&R reduces the vulnerability compared with naïve fish and fish only exposed to angling associated disturbance, but not to the same extent as fish with private experience of hooking; and (b) the physiological stress response will reflect the angling experience that fish have been subjected to, i.e. the highest stress response is expected in fish with private experience of angling, followed by fish with social experience and be the lowest in naïve fish.
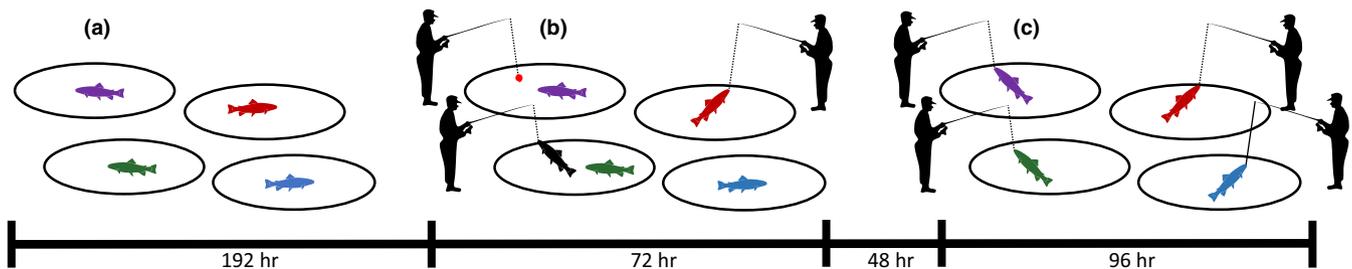

FIGURE 1 Schematic figure of experimental set-up with the different angling treatments in each pond. Blue = Control; Purple = Disturbance; Red = Private; Green = Social; and Black = demonstrator fish from the non-experimental pond used in the social exposure treatment. (a) Acclimation period before angling, (b) Angling exposure treatment and (c) Vulnerability assessment when all ponds were fished. Timeline represents the duration in hours for each period as well as the resting time between the angling treatments and vulnerability assessment [Colour figure can be viewed at wileyonlinelibrary.com]

2 | METHODS

2.1 | Experimental design

To evaluate the relative contribution of private versus social experience of fish to angling, a triplicated angling experiment was conducted in four semi-controlled ponds stocked with size-matched rainbow trout. The experiment consisted of two steps: first the angling exposure treatments (Figure 1b) followed by a period of angling trials during which catch rates were quantified and compared across treatments, and served as a vulnerability assessment of fish to the different levels of angling exposure they had been subjected too (Figure 1c). The angling exposure consisted of four treatments (Figure 1b): (a) a private exposure treatment during which fish were caught and released back to the same pond to ensure the private experience of angling; (b) a social exposure treatment where fish experienced only the social stimuli of other conspecifics fighting on the line; (c) a control: where fish had no exposure treatment and remained naïve to angling; and (d) a second control treatment called disturbance treatment with fish exposed to hook-less angling gear to account for the possible effects of the disturbance related to the angling method itself. The experiment was repeated three times between 8 September and 9 November 2016. To control for possible pond effects, the treatment order was changed between experimental rounds so that no treatment was repeated within the same pond. Additionally, stress response of fish was assessed by implanting a subset of fish in the last round of the experiment with heart rate loggers, recording changes in heart rate as a proxy of stress response of fish to angling treatments. The experiments were approved by the Ethical Committee for Animal Research of the University of Gothenburg (Licence 15.2014 and licence 165–2015) and comply with Swedish and European law.

2.2 | Experimental set-up and fish

The study was conducted in the facilities of the Swedish sport fishing association (Sportfiskarna) at Sjölyckan, Gothenburg, Sweden. The experimental system consisted of four ponds (30 × 24 × 2 m; $L \times W \times D$, 1,440 m^2 each) with a constant inflow from Lake Delsjön (mean temperature ± SD: round 1:18.1 ± 1.0°C; round 2:12.0 ± 2.0°C; round 3:7.8 ± 0.9°C). Prior to the experiment, the ponds were drained and cleaned from macrophytes and debris, then stocked before each experimental round with size-matched rainbow trout (163 fish per round; mean ± SD: mass = 391.6 ± 55.1 g; fork length = 31.6 ± 1.5 cm) transported from the Källefall hatchery (58°10′12.3″N 14°4′47.6″E). On arrival, fish were settled for at least an hour in holding tanks (2 × 2 × 0.5 m; $L \times W \times D$) supplied with aerated Lake Delsjön water at ambient temperature, then anaesthetised (in round 1 and 3: MS-222 at 150 mg/L buffered with $NaHCO_3$ at 300 mg/L; in round 2: benzocaine 400 mg/L), measured for mass and fork length and tagged with a passive integrated transponder (PIT; 23 × 3.65 mm, 0.6 g, Texas Instruments) to enable individual identification. PIT-tags were inserted into the abdominal cavity through a small incision and followed by cutaneous application of an antiseptic paste (Vetofish, SELARL Vétérinaire). Following tagging and surgical implantation, fish were placed in a recovery tank (1 × 1 × 0.5 m; $L \times W \times D$) for observation. When each fish had resumed normal swimming and respiratory motion, they were distributed randomly among the four experimental ponds and left to acclimate for 8 days (Figure 1a). No difference in mass was found between the treatments following the random pond distribution (ANOVA: F = 0.486, p > 0.05 for all comparisons). No food was provided during the experiment, but naturally occurring invertebrates such as Trichoptera were present in the ponds.

2.3 | Heart rate logger implantation

To measure the stress response in fish during the different angling exposures, a subset of 30 individuals in round 3—equally distributed between social exposure, private exposure and control treatment—were surgically implanted with bio-loggers (39.5 × 13 mm and 11.8 g, DST milli-HRT, Star-Oddi) capable of measuring time-stamped (accuracy ± 1 min/month) heart rate and temperature (resolution 0.032°C, accuracy ± 0.2°C). These fish are from here on referred to as the heart rate logger-fish. For consistency between treatments, since in the disturbance exposure treatment no fish received a bio-logger, a subset of 10 individuals were sham operated, which means that they underwent identical surgical treatment as the heart rate logger-fish, but no bio-loggers were implanted.

The bio-loggers were programmed to derive an average heart rate from 6-s-long measures of electrocardiogram (ECG) sampled at a frequency of 100 Hz. The bio-loggers were programmed to record at two different sampling frequencies: one high-frequency period (one measurement per min) that covered the 5 hr around the angling trials between 13:30 and 18:30 (see below for details) and one low-frequency period (one measurement per 10 min) that covered the other 19 hr of the day. For validation purposes, all logged heart rate measurements are graded with a data verification quality index (QI) by the software supplied by the manufacturer, ranging from 0 to 3, whereby QI0 = Great, QI1 = Good, QI2 = Fair and QI3 = Poor. To ensure the highest possible accuracy, only measurements graded with QI0 were used in the present study following Brijs et al. (2018) and Brijs et al. (2019).

Before implantation of the bio-loggers, the fish were individually anaesthetised in MS-222 as described above. When the fish had lost equilibrium and stopped ventilating, each was positioned on its side on water-soaked rubber foam on a surgical table. During the surgery, the gills were continuously flushed with aerated 10°C water containing 75 mg/L MS-222 and 150 mg/L $NaHCO_3$ to maintain anaesthesia. The bio-loggers were inserted through a ~30-mm incision along the mid-ventral line approximately 40 mm posterior to the pectoral fins, and positioned longitudinally in the pericardial cavity and anchored to the muscle, following Brijs et al. (2018) and Ekström, Axelsson, Gräns, Brijs, and Sandblom (2018).

2.4 | Angling exposure treatments

Following the 8-day acclimation period, fish from each pond were exposed to different angling treatments (Figure 1b). The initial sample size in each treatment was set to 40 except for the social exposure (*n* = 43; see social exposure treatment section). In each round, all exposure treatments were conducted simultaneously for 1 hour of angling per day on three consecutive days.

In the private exposure treatment, the aim was to evaluate how the private experience of being caught and released affected the stress response and angling vulnerability. Two experienced anglers, placed on each short side of the pond, used a spinning rod (braided line: resistance 4.5 kg; 1 m fluorocarbon leader, resistance 4.9 kg; and barbless hook [Gamakatzu G-code, Worm 39, Size 3]) baited with a dead shrimp. Anglers chose freely where to cast, how long to keep the bait at one spot and the depth at which the bait was presented. Caught fish were landed as quickly as possible and transferred with a knotless landing net to a water-filled bucket, to be unhooked and identified. During the remainder of the angling event, the caught fish were kept in recovery tanks (1 × 1 × 1 m; *L* × *W* × *D*) with a constant refill of aerated water. Immediately after the angling event, all fish caught were transferred back to their corresponding 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. In the event of deep-hooking, fish were euthanised with a sharp blow to the head.

In the social exposure treatment, the aim was to evaluate the effect on vulnerability and stress by exposing the fish to the social stimuli of other conspecifics being hooked and fighting on the line. To ensure that the fish experienced the social stimuli of other individuals being hooked, each daily exposure began with an angler catching one fish in the pond. 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 a non-experimental pond. This procedure was done to reduce the risk of confounding effects from catching all the vulnerable fish first while leaving less vulnerable fish within the pond (Koeck et al., 2019). During the remainder of the social exposure, rainbow trout not used in the experiment were caught in the non-experimental pond and gently transferred to the treatment pond where they were displayed for approximately 30 s, fighting freely in the pond while on the angler's line. After the display, the fish were transferred back to the non-experimental pond and a new fish was caught for display. 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 (total captures in round 1; *n* = 37, round 2; *n* = 41, round 3; *n* = 39). The purpose of this procedure was to expose the fish to a similar level of disturbance/opportunity to acquire social information about fishing threat, as experienced directly by individuals in the private exposure treatment, without providing any focal fish with private experience of C&R. The difference in initial sample size between the social exposure and the other angling treatments (43 compared to 40 per replicate) was set to compensate for the daily removal of one individual.

A disturbance treatment was included in the experimental design to account for the possible effects of disturbance related to the angling method itself, that is, likely non-threatening disturbance caused by casting and retrieving the tackle and the anglers' movements around the ponds. The disturbance treatment was performed in the same way as in the private exposure treatment but without using bait or hooks. No angling was conducted in the control treatment.

2.5 | Vulnerability assessment

Forty-eight hours after the last day of angling exposure treatment (Figure 1b), standardised angling was conducted simultaneously in all experimental ponds for 1 hour during four consecutive days (Figure 1c). Two experienced anglers were randomly allocated to each pond, with one angler positioned on each short side of the pond. Every tenth minute, the anglers changed ponds and position to randomise differences in fishing technique and skills. As in the private exposure treatment, barbless hooks baited with shrimp were used. Fish caught were kept in recovery tanks during the remainder of the angling event and, after identification, released back to their respective ponds. Each individual thus could potentially be caught up to four times. When one round of angling was complete, the ponds were drained and the fish were sampled for mass and length measurements, before the ponds were refilled and stocked with a new batch of fish for the next experimental round following the same procedure. The time of day 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.

2.6 | Data handling and statistical analysis

All data subjected to statistical analyses were assessed to ensure that they did not violate the assumptions of the models used. A Cox proportional hazard regression ("coxph" function, "survival" package, R) was modelled to analyse associations between treatment and time-to-event, i.e., to what degree the angling exposure treatments affected the chances of an individual being caught over time. The model accounted for only one event per individual, i.e., the response variable was the time until first catch. Because of the marked decrease in water temperature over the course of the experiment, temperature (instead of round) was added as a covariate to the survival model. Non-significant interaction between temperature and treatments indicated, however, that temperature did not affect catch rate in a specific treatment, and the interaction term was thus excluded from the final model (Table 1). Furthermore, not all individuals in the private exposure treatment were caught during the exposure angling (proportion caught fish round 1; 0.8, round 2; 0.825, round 3; 0.75). Since uncaught individuals in the private exposure treatment lacked private experience of C&R, they were discarded from the main analysis.

To quantify heart rate response to angling, an individual hourly mean heart rate was calculated and used in further analyses. The

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TABLE 1 Cox proportional hazard regression, estimating the effect of treatment and temperature on the time individuals remained uncaught during the vulnerability assessment. Control treatment is the reference level. The number of events refers to the total number of caught fish

Parameter	Estimate	Exp(coef)	Se(coef)	z-Value	p-Value
Disturbance	−0.0924	0.9116	0.1422	−0.605	0.515
Social Exp.	−0.2672	0.7654	0.1445	−1.849	0.064
Private Exp.	−1.2968	0.2733	0.1907	−6.799	**<0.001**
Temperature	0.0264	1.0267	0.0125	2.104	**<0.05**

Note: n = 411, number of events = 328. Likelihood ratio test = 68.21 on 4 *df*, $p < 0.001$. Significant *p*-values < 0.05 are indicated in bold.

effects of angling disturbances on heart rate following the three periods (i.e., acclimation period, angling exposure and vulnerability assessment) were investigated using a linear mixed model. In this model, hourly mean heart rate was used as dependent variable. Angling exposure treatment, period and day were included as fixed factors. Fish ID and hour of day were used as random effects. In this analysis, heart rates recorded between the start of an angling period and the following 24 hr (i.e., 15:00–15:00) were defined as a day, so that the acclimation period included the last 3 days and angling exposure, and vulnerability assessment included three and four separate days, respectively. The heart rate data were analysed using SPSS Statistics 22 (IBM Corp.).

3 | RESULTS

3.1 | Effects of angling exposure on subsequent vulnerability to angling

Across all treatments, the private exposure treatment had the most pronounced effect on subsequent catchability and significantly reduced capture vulnerability by 72.6% relative to fish from the control treatment (Table 1, Figure 2). The social exposure treatment produced a non-significant decrease in angling vulnerability of 23.4% relative to fish in the control treatment (Table 1, Figure 2). Fish in the disturbance treatment reduced angling vulnerability by only 8.9% relative to control treatment, which was not significant (Table 1, Figure 2). Capture vulnerability generally increased with temperature (Table 1), which did not interfere with exposure treatment (non-significant interaction; see method section). No difference in catch rate was found between the sham, control and private heart rate logger-fish when comparing proportions of individuals caught for the first time (χ^2 = 1.14, *df* = 2, $p > 0.05$), indicating that the implantation procedure and presence of heart rate logger did not bias the catch rate results.

3.2 | Heart rate response to angling treatments

No difference in heart rate was found between the private exposure and control treatment during the acclimation period (Table 2, Figure 3a). However, during the two last days of the acclimation period, the heart rates in the social exposure were significantly higher than the control treatment, while private exposure and social exposure showed no differences in their heart rates (Table 2, Figure 3a). During the first day of angling exposure, a pronounced
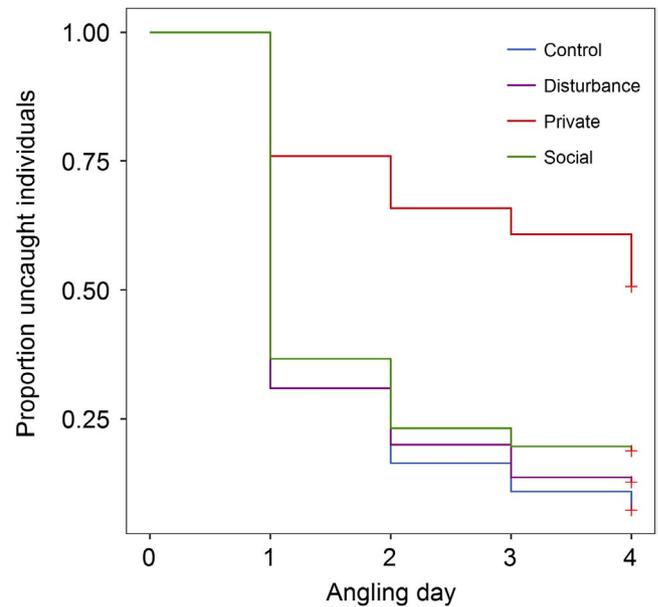

FIGURE 2 Survival curves based on the Cox proportional hazard regression model, illustrating the remaining proportions of uncaught individuals across days, for the four exposure treatments (Blue = Control; Purple = Disturbance; Red = Private; and Green = Social) during the vulnerability assessment. Day 0 denotes the day before angling, and day 4 denotes the last angling day [Colour figure can be viewed at wileyonlinelibrary.com]

significant increase in heart rate in the private exposure treatment was found, while an intermediate significant increase was seen in the social exposure treatment relative to the control treatment (Table 2, Figure 3b). During the second and third day of angling exposure, the peak heart rate response in the private exposure treatment was somewhat reduced relative to the first treatment day, such that the private exposure treatment was not significantly different from the social exposure treatment (private *vs* social; mean daily difference in heart rate ± *SE*, *p*-value; Day 1:3.19 ± 0.70, $p < 0.001$; Day 2:0.07 ± 0.68 $p = 0.91$; Day 3:0.74 ± 0.68 $p = 0.28$; Figure 3b). However, both the private and social exposure treatments had a significantly higher heart rate than the control treatment during all 3 days of angling treatment (Table 2, Figure 3b). When analysing the daily effects of angling on heart rate across treatment groups, all three treatments differed significantly during the first day of vulnerability assessment (Social >Private >Control: Table 2, Figure 3c). In the subsequent days, the peak heart rate response during angling was gradually reduced in all treatments, and during the last 2 days of vulnerability assessment, no difference in heart rate was found

Period	Day	Parameter	Estimate	Std. Err	Df.	*t*-Value	*p*-Value
Acclimation	1	Intercept	67.80	4.202	577.63	16.13	**<0.001**
		Private	0.75	0.562	647.46	1.34	0.179
		Social	0.11	0.599	647.49	0.19	0.848
Acclimation	2	Intercept	65.62	4.610	508.57	14.23	**<0.001**
		Private	0.51	0.620	651.67	0.82	0.408
		Social	1.36	0.656	651.67	2.07	**<0.05**
Acclimation	3	Intercept	59.86	5.929	263.84	10.09	**<0.001**
		Private	1.31	0.808	425.66	1.63	0.104
		Social	1.82	0.857	425.70	2.13	**<0.05**
Exposure	1	Intercept	49.75	4.964	189.18	9.41	**<0.001**
		Private	6.94	0.676	656.95	10.26	**<0.001**
		Social	3.75	0.716	656.95	5.23	**<0.001**
Exposure	2	Intercept	34.19	4.445	13.92	7.69	**<0.001**
		Private	5.49	0.658	647.58	8.35	**<0.001**
		Social	5.42	0.699	647.95	7.75	**<0.001**
Exposure	3	Intercept	51.23	4.880	296.20	10.49	**<0.001**
		Private	4.32	0.661	660.97	6.54	**<0.001**
		Social	3.58	0.701	660.98	5.11	**<0.001**
Vulnerability	1	Intercept	39.77	5.203	58.41	7.64	**<0.001**
		Private	3.12	0.725	663.80	4.30	**<0.001**
		Social	5.08	0.770	663.65	6.60	**<0.001**
Vulnerability	2	Intercept	30.69	4.013	3.71	7.64	**<0.01**
		Private	2.30	0.649	625.28	3.54	**<0.001**
		Social	2.98	0.688	622.61	4.32	**<0.001**
Vulnerability	3	Intercept	38.48	4.792	49.16	8.03	**<0.001**
		Private	0.55	0.674	658.89	0.82	0.408
		Social	0.76	0.715	658.37	1.06	0.287
Vulnerability	4	Intercept	24.92	0.631	234.21	39.47	**<0.001**
		Private	1.36	0.651	619.00	2.10	**<0.05**
		Social	0.43	0.673	619.00	0.650	0.516

Note: Control treatment was used as reference levels. Fish ID and time were used as random effects.

Significant *p*-values < 0.05 are indicated in bold.

between the treatments except between private and control treatment during the final day (Table 2, Figure 3c). Cardiograms of all individual fish are provided in supplementary Figure S1.

4 | DISCUSSION

The private experience of C&R was found to be the main contributor to decreased vulnerability in rainbow trout and individuals caught demonstrated a more distinct physiological stress response (Anderson et al., 1998), as indicated by elevated heart rate compared with uncaught individuals. This is in agreement with previous studies on decreased catch rate and catchability in C&R recreational fisheries (e.g., common carp: Beukema, 1970a; Klefoth et al., 2013; rainbow trout: Askey et al., 2006; van Poorten & Post, 2005; and brown

trout, *Salmo trutta* L.: Young & Hayes, 2004). The present results also indicated that social experience and angling disturbance do not significantly contribute to decreased vulnerability in C&R fisheries for rainbow trout. However, the results suggested that the social experience of hooked conspecifics alone suffices to induce an increase in heart rate, providing evidence of a cardiovascular stress response in rainbow trout to social experience of C&R.

Fish that had previously experienced hooking (i.e., fish from the private exposure treatment) were caught substantially less frequently than fish indirectly exposed to angling (i.e., socially experienced fish) and fish naïve to angling (i.e., from the control treatment). This suggests that additional mechanisms (e.g., physiological and behavioural) not quantified here are affecting vulnerability. Possible factors that were unique to previously hooked fish that might explain their increased subsequent hook avoidance relative
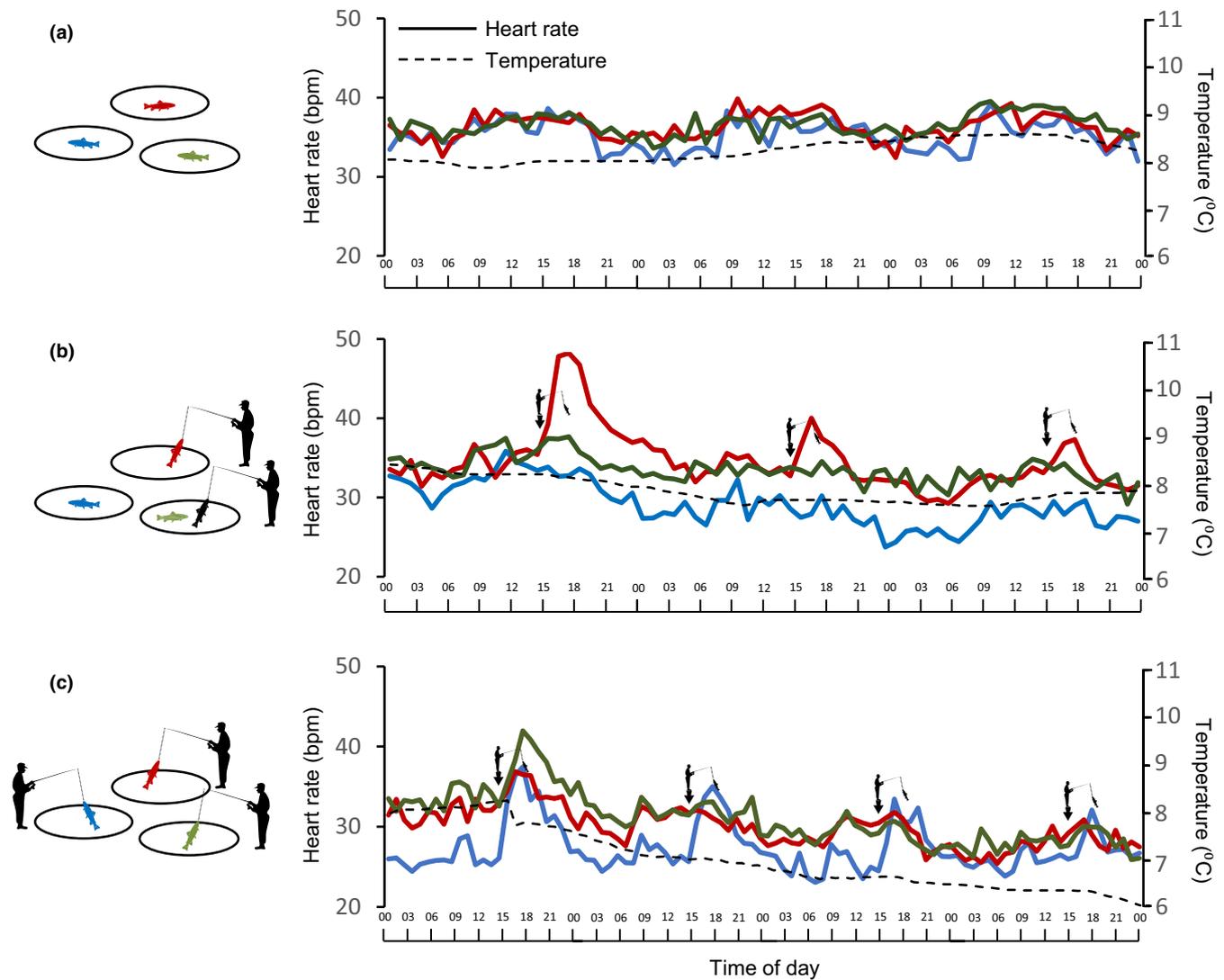
FIGURE 3 Mean heart rate per treatment following acclimation period, angling exposure and vulnerability assessment. Statistical change in heart rate was analysed from the start of an angling period (symbolised by the angler) until the following angling event (15:00–15:00). (a) Acclimation period before angling, (b) Heart rate during the angling exposure treatment and (c) Heart rate during the vulnerability assessment. (Blue = Control; Red = Private; Green = Social) [Colour figure can be viewed at wileyonlinelibrary.com]

to fish in the social exposure treatment include the following: repeated visual stimuli of other conspecifics being hooked, combined with hook injury, physical exhaustion and air exposure, which have been found to result in elevated plasma levels of stress indicators, such as cortisol and glucose (Arlinghaus, Klefoth, Cooke, Gingerich, & Suski, 2009; Cooke et al., 2001; Donaldson et al., 2010; Pullen et al., 2017). Moreover, it is possible that these factors triggered a tertiary stress response in the privately hooked fish (Barton, 2002; Wendelaar Bonga, 1997), leading to behavioural changes following C&R (Arlinghaus et al., 2009; Halttunen et al., 2010; Klefoth et al., 2011; Schreer, Resch, Gately, & Cooke, 2005). In addition, the reduced heart rate displayed during the subsequent days in the private exposure treatment may also indicate that fish habituated to the stressor of C&R angling (Barton, Schreck, & Barton, 1987). However, the continuous decrease in heart rate in the private exposure treatment might also have been related to the gradual

decrease in water temperature (Eliason & Anttila, 2017), as indicated by the continuous decrease in heart rate in the control group.

The present study was conducted with hatchery fish, which represent both a strength and a limitation. First, hatchery fish are a suitable model when studied in semi-natural environments such as the ponds used here because they are likely better adapted to ponds compared to wild conspecifics. The greater degree of domestication of hatchery-reared fish and the associated adaptation to stressful situations during handling (Woodward & Strange, 1987) seems to increase the readiness to take baits presented by anglers compared with wild fish (Koeck et al., 2019; Mezzera & Largiadèr, 2001). Indeed, the rainbow trout used in the present study have been artificially selected since the 1990s (personal communication with Källefall Hatchery), which has probably favoured bold and stress-resistant phenotypes (Berejikian, 1995; Biro & Post, 2008; Johnsson & Abrahams, 1991), while decreasing the overall

phenotypic variation compared with a wild population (Fleming & Einum, 1997). As learning capacities might differ between individuals within a population, some individuals might rely on social information to a higher degree (Lucon-Xiccato & Bisazza, 2017). Thus, the use of hatchery fish, which have been selected for bold phenotypes, could have influenced the importance of social information transfer, which potentially could be more important in wild populations with less bold phenotypes.

There are also other reasons that could have reduced the importance of social information transfer on subsequent vulnerability in the present study. Importantly, in addition to the direct experience of being hooked, fish in the private exposure treatment were surrounded by other fish with previous hook experience, whereas fish in the social exposure treatment only briefly experienced already hooked individuals. Experienced individuals could act as demonstrators (Johnsson & Sundström, 2007; Kelley, Evans, Ramnarine, & Magurran, 2003; Vilhunen, Hirvonen, & Laakkonen, 2005), reinforcing the hook avoidance behaviour in other individuals during the final vulnerability assessment. The behavioural influences of social learning could thus be stronger in conditions where hooked fish are present, in contrast to the experimental conditions induced. However, in the absence of such experimental information, this present work on rainbow trout joins a related paper on largemouth bass (Wegener et al., 2018), suggesting that social learning to avoid future capture may not be strongly expressed in hatchery-reared rainbow trout. Whether social learning exists in wild trout constitutes an important question for the future.

In conclusion, the results presented in the current study show that social exposure to caught individuals can transmit sensory information that is received by nearby observers and translated into a stress response. However, such stress responses were not strong enough to cause significant declines in subsequent vulnerability to angling. By contrast, private experience of hooking strongly affected subsequent vulnerability to capture, which can negatively affect angler satisfaction (Arlinghaus, Beardmore, Riepe, Meyerhoff, & Pagel, 2014; Beardmore, Hunt, Haider, Dorow, & Arlinghaus, 2015) and reduce the ability of managers to assess fish stocks based on catch rate data alone (Arlinghaus et al., 2017). This study adds a mechanistic insight into the repeated empirical observation that continued C&R angling will lead to a drop in catchability. These declines in catch rates constitute a challenge to fisheries managers interested in maintaining high catch rates for the benefits of anglers (Camp, Poorten, & Walters, 2015). Previous studies suggesting effects of social learning on catch rates (e.g., Beukema, 1970b, Raat, 1985) may indicate either species-specific effects or the need for continuous presence of demonstrators with private experience for social learning to exert an impact on catch rates.

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