Does parental angling selection affect the behavior or metabolism of brown trout parr?

Running title: Angling selection and brown trout behavior

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Abstract

The behavior of organisms can be subject to human induced selection such as that arising from fishing. Angling is expected to induce mortality on fish with bold and explorative behavior, which are behaviors commonly linked to a high standard metabolic rate. We studied the transgenerational response of brown trout (*Salmo trutta*) to angling-induced selection by examining the behavior and metabolism of 1-year-old parr between parents that were or were not captured by experimental fly fishing. We performed the angling selection experiment on both a wild and a captive population, and compared the offspring for standard metabolic rate and behavior under predation risk in common garden conditions. Angling had population-specific effects on risk taking and exploration tendency, but no effects on standard metabolic rate. Our study adds to the evidence that angling can induce transgenerational responses on fish personality. However, understanding the mechanisms of divergent responses between the populations requires further study on the selectivity of angling in various conditions.

Introduction

Survival selection by hunting and fishing can differ from natural selection patterns and induce phenotypic changes in various traits over time (Fugère and Hendry 2018). At worst, anthropogenic selection can increase the relative frequencies of maladaptive phenotypes decreasing the fitness of harvested populations (Allendorf and Hard 2009; Coltman et al. 2003). Experimental studies have shown that responses to human-induced selection can be rapid at both phenotypic, including behavior (Kern et al. 2016; Sbragaglia et al. 2019; Wong et al. 2012) and genetic levels (Bowles et al. 2020; Cooke et al. 2007; Sutter et al. 2012; Uusi-Heikkilä et al. 2015). Fisheries-induced selection can occur on traits that explain vulnerability to fishing and on traits that enable the fish to reproduce before becoming captured (Cooke et al. 2007; Hollins et al. 2018; Redpath et al. 2010; Sutter et al. 2012; Uusi-Heikkilä et al. 2008).

In the context of recreational fisheries, selection is predicted to act mainly on behavior, as the vulnerability to being captured depends on fish behavior, and capture leads to either survival costs or other non-lethal fitness costs (Lennox et al. 2017; Uusi-Heikkilä et al. 2008). Vulnerability to capture by passive fishing gear, including angling, depends on traits related to risk-taking and curiosity, such as boldness and exploration tendency (Arlinghaus et al. 2017; Cooke et al. 2007; Härkönen et al. 2014; Wilson et al. 2015, reviewed in Lennox et al. (2017)), although not all studies have supported the predicted role for boldness (Louison et al. 2017; Vainikka et al. 2016). Over time, angling selection could increase the frequency of shy phenotypes in the population (Alioravainen et al. 2020a; Andersen et al. 2018; Arlinghaus et al. 2017). The shift in the behavior of fish populations may occur on top of the fishing/angling-induced decrease of body size and age-at-maturity (Bowles et al. 2020; Sharpe and Hendry 2009) and cause a personality-related decrease in resource acquisition.

Eventually, these can lead to complex effects on stock recruitment (Arlinghaus et al. 2017). However, these predictions for the existence and consequences of increasing shyness due to passive fishing gear require further empirical tests.

Selection acting on personality could induce correlated metabolic effects due to physiological covariation between behaviors affecting energy balance and standard metabolic rate (SMR) (e.g., Mathot et al. 2018; Killen et al. 2011). In one of the first empirical angling selection studies, SMR was found to be 10% lower in a low-vulnerability selection line compared to a high-vulnerability selection line in largemouth bass (*Micropterus salmoides*) (Redpath et al. 2010). However, several studies have found no phenotypic association between angling vulnerability and SMR (Väätäinen et al. 2018), or between angling vulnerability and several metabolic traits, including SMR (Louison et al. 2017; Louison et al. 2018). Given that metabolic traits are are also sensitive to environmental conditions, and angling methods may impose different selection pressures in different experiments, the potential for evolutionary response in metabolic traits in response to angling-induced selection is presently not well understood.

Salmonids, just as many other taxa, can display individually distinctive behavioral strategies and coping styles (Adriaenssens and Johnsson 2011; Brelin et al. 2008; Huntingford and Adams 2005; Näslund and Johnsson 2016; Vindas et al. 2017), on which selection may act. Due to their widespread hatchery rearing, species such as the brown trout are also affected by unintended domestication, introducing shifts in life-history traits, behavior (Araki et al. 2008; Horreo et al. 2018; Huntingford 2004) and vulnerability to angling (Klefoth et al. 2013); more research on the effect of unintended domestication on fish populations used in supplemental releases is therefore warranted.

83 Here, our goal was to test whether angling could induce selection in behavioral traits
84 measured under authentic predator cues or in SMR by studying one-year-old offspring of
85 brown trout (*Salmo trutta*) from both captive and wild origins. By using replicated behavioral
86 assays involving predator cues and collecting metabolic rate data, we add to the study by
87 Alioravainen et al. (2020a), which focused on open-field tested personality of the offspring
88 from the same angling experiments during their first summer. We further compared fish
89 acclimated under 12h light:12h dark or 24h light, because unnatural light conditions may be
90 perceived as stressful by the fish and modify the phenotypic responses. We hypothesized that
91 offspring from angling-vulnerable parents would have higher scores in risk-taking behavior,
92 and higher SMR, compared to fish from non-vulnerable parents in both strains of fish.
93

94 **Material and methods**

95 *Angling experiment and fish husbandry*

96 Experiments were carried out between 2015 and 2017 at the Kainuu Fisheries Research
97 Station (www.kfrs.fi) of Natural Resources Institute Finland (Luke) under ethical license
98 obtained from the national Animal Experiment Board in Finland (license number
99 ESAVI/3443/04.10.07/2015). We used 1) wild, predominantly non-migratory, parental brown
100 trout from River Vaarainjoki captured by electrofishing, and 2) captive (5–6th generation),
101 predominantly migratory brown trout from so-called Lake Oulujärvi hatchery strain. The
102 founders of the captive brood stock came from two source populations, River Kongasjoki and
103 River Varisjoki (Lemopoulos et al. 2019a; Alioravainen et al. 2020a). Despite originating
104 from the same River Varisjoki watershed, only a few km apart, the captive and R. Vaarainjoki
105 populations showed moderate genetic divergence based on fixation index (F_{ST}-value) of 0.11
106 (Lemopoulos et al. 2019a). Both populations had experienced fishing pressure (mainly hook-

107 and-line fishing) in the past, but not since R. Vaarainjoki was protected from fishing in the
108 1990s and the original captive population was established in the 1960s-80s.
109
110 In 2015, hatchery-origin and wild-origin adult fish were exposed to experimental fly fishing
111 and divided into captured (high vulnerability, HV) and uncaptured (low vulnerability, LV)
112 groups (Fig. 1) (Alioravainen et al. 2019a). Fish were fished in two size-assortative pools for
113 each population during June and July with fly fishing gear adjusted by the size of the fish in
114 the pools. The wild fish were fished in semi-natural 50-m^2 ponds with a gravel-bottom outer
115 riffle sections and *ca*. 1 m deep, concrete inner pool sections (53 and 91 visually size-sorted
116 fish in two ponds). The hatchery fish were fished in 75-m^2 concrete ponds with no structures
117 (64 larger and 167 smaller fish from two different cohorts in two ponds). Angling was
118 performed by experienced fly fishers (mainly A.V.) using unnaturally colored woolly bugger -
119 type fly patterns tied to barbless hooks. During angling sessions, an angler fished a pond until
120 a fish took the fly or five minutes passed, after which angling was continued at earliest one
121 hour later. If a fish was captured, angling was continued immediately after processing, which
122 included anesthesia with benzocaine (40 mg L^{-1}), identification of passive integrated
123 transponder (PIT) tag (Oregon RFID), or tagging when a pre-existing tag was missing, and
124 measuring total length (to 1 mm) and weight (to 2 g). Fish that were missing PIT-tags were
125 tagged under the skin next to the dorsal fin using 12 mm tags at this point. After processing,
126 the fish were transferred to similar ponds (hatchery fish to a 50-m^2 otherwise similar concrete
127 pond) as used for each population during angling. After angling trials were finished, on 25
128 June 2015, all remaining wild fish that were not captured were collected by dip-netting after
129 draining the experimental angling ponds, anaesthetized, measured and weighed (mean body
130 lengths of fish uncaptured and captured by angling: in large fish 457 and 475 mm,
131 respectively, and in small fish 344 and 354, respectively). Uncaptured wild fish were then

132 combined in the same ponds as the fish captured by angling. The captured hatchery strain fish
133 were subjected to a second round of angling ~2 weeks later to identify the most vulnerable
134 fish, where in total eight fish were captured and prioritized for breeding the highly vulnerable
135 line, but this was not done on wild fish due to their limited availability. Angling trials finished
136 on 8 July 2015, and also hatchery fish were transferred back to their original ponds. Because
137 of the warm water at the time of finishing the second round of angling, the uncaptured
138 hatchery fish were not measured to avoid handling-induced stress and mortality. One deep-
139 hooked small hatchery fish was found dead 5 days and one large hatchery fish 41 days after
140 capture, but otherwise no mortality occurred between angling trials and the breeding.
141
142 From the hatchery stock, 32.8 and 50.9% (corresponding to 21 and 85 fish), and from the wild
143 stock, 28.3 and 24.2% (corresponding to 15 and 22 fish) of large and small individuals were
144 captured, respectively. Notably, the wild fish had natural invertebrate food available in their
145 ponds, and the structured ponds offered more hiding places, and they had clearly lower
146 catchability than the hatchery fish (Alioravainen et al. 2020a). Very few wild fish were
147 captured in one angling session (maximum 4) compared to the hatchery fish (maximum 11).
148 The captured and non-captured parent fish were similar in size, indicating that vulnerability to
149 angling was most likely related to size-independent traits (Alioravainen et al. 2020a).
150
151 The offspring used in this study were obtained from fish bred in four groups (i.e. high- and
152 low-vulnerability [HV and LV, respectively] within each population) in the autumn of 2015.
153 Parent fish from large and small size groups were mixed for breeding. A replicated, fully
154 factorial 3 × 3 breeding design was used to create the F_1-generation; males were crossed with
155 females in all combinations in one matrix, and the matrices replicated three times for each
156 group, details in Appendix A, and in Alioravainen et al. (2020a). In the autumn of 2016, the

one-summer-old fish were tagged with individual 12-mm PIT-tags in the abdominal cavity under anesthesia (benzocaine). After tagging, the selection lines were mixed together in two 3.2 m^2 fiberglass rearing tanks. During the whole study, fish were fed with commercial fish pellets (Raisio Oyj).

Photoperiod acclimations

In mid-March 2017, after being reared under constant light, 100 fish were divided into two different photoperiod treatments in 0.4-m^2 green, plastic, flow-through tanks. The tanks were covered with green nets. One treatment continued to be reared under constant light (approximately 9 lux at the water surface, n = 10/selection line/population, 40 fish in the tank), and the second treatment received a 12h light:12h dark (L:D) acclimation (approximately 12 lux during light period at the water surface, N = 15/selection line/population divided equally in two tanks, details in Appendix A).

Fish were fed using automatic belt feeders (~0.3% fish mass per day) on 5–6 days per week during approx. 4h between 8:00 and 20:00 to avoid the entrainment of endogenous rhythms by feeding. After a minimum two-week acclimation, the metabolic rate measurements were started.

Measurement of standard metabolic rate

The SMR, i.e., post-absorptive, resting O_2 uptake ($\dot{M}O_2$) (Nelson 2016)), of fish was measured using intermittent flow-through respirometry (Svendsen et al. 2016). The fish were not fed for 40–48h before the start of the measurement to minimize the effect of digestion on metabolic rate. As fish from the same tank were measured on multiple days, fish in each tank were fed on a rotation of 40–48h fasting followed by 1.5 d of feeding. The fish were caught by dip-netting

182 under a dim red light into 10-L buckets, identified with a PIT-reader and transferred to the flow-
183 through measurement chambers (diameter 33 mm, length 120 mm, Loligo Systems, Viborg,
184 Denmark). The chambers were immersed in a water bath, which was also immersed in a flow-
185 through tank. Measurements were started immediately and continued for approximately 23h,
186 corresponding to 90–96 15–17-min measurement cycles for all individuals. We measured 2–4
187 individuals in separate horizontal glass chambers during each day of measurements. Oxygen
188 saturation was measured in % of air saturation using two-point-calibrated DAQ-PAC-WF4
189 system with Sensor spot mini sensors and recorded every second in AutoResp software (Loligo
190 Systems). Water temperature was measured using the Pt1000 temperature probe placed in the
191 respirometer tank (Loligo Systems). Air pressure in kPa, with one decimal, was recorded daily
192 at the start of measurements from a nearby weather station.
193
194 The respirometry measurements were started between 11:45 am and 12:10 pm by measuring
195 the oxygen level in each empty chamber for one cycle to establish a baseline for bacterial
196 oxygen consumption. The cycles consisted of a 6-min flush and a 9–11-min recirculation
197 period, including a 5.5–7.5-min wait period to allow mixing of the water and a 3.5-min
198 measurement. The temperature in the acclimation tanks was on average 3.4°C ± SD 0.12°C
199 during the respirometer measurements, but the respirometer temperature was slightly higher
200 than the acclimation temperature (range 3.4–4.2°C) due to the unavoidable heating of the tank
201 by the measurements. During the measurement, the respirometer was covered with a green net,
202 similar to what was used to cover the acclimation tanks prior to measurements, and disturbances
203 were kept to a minimum. The fish were passive for extended periods of time during the
204 measurements (observed from oxygen measurements). The chambers were washed using mild
205 Deconex disinfectant and the water inside the respirometer tank was changed every 5-7 d during
206 the measurements. Six measurements, where air bubbles were observed in the measurement

207 chamber, were discarded from the analysis. The photoperiod was 12h:12h L:D during
208 respirometry for all fish, because the lowest consumption was expected to occur during the dark
209 phase.
210
211 After measurements, fish were anesthetized with benzocaine, measured for total length (to 1
212 mm) and weighed (to 0.1 g), after which they were transferred to new 0.4 m^2 tanks similar to
213 those used prior to measurements. The fish were under the same photoperiod as before the
214 measurements and fed daily at varying times. After removing the fish, respirometer chamber
215 oxygen levels were measured empty for one cycle to quantify bacterial respiration rates. No
216 measurable respiration was detected without fish. The slope of the decrease in oxygen level
217 during each 3.5-minute measurement period was calculated using linear regression with
218 FishResp (Morozov et al. 2019) in R. An initial acclimation period was excluded by including
219 only measurements taken after 16:00 in the analysis. We accepted all slopes where the R^2 was
220 > 0.9 in the calculation: this resulted in 12–70 slopes being accepted for each individual, after
221 data from one individual with only 7 accepted slopes was excluded. R code for analyzing the
222 raw data is provided in GitHub (see Data availability).
223
224 The SMR was calculated as the average $\dot{M}O_2$ across all accepted cycles after comparing data
225 obtained using several methods following Chabot et al. (2016): quantile 0.1, quantile 0.2,
226 lowest 10 consumption values, and average. The average of accepted cycles was used as it
227 was the only variable that showed a positive mass-dependence of metabolic rate. Other
228 variables were not correlated with fish body mass, likely indicating inconsistencies in fish-
229 specific accepted measurements due to variation in R^2 values. The average of accepted cycles
230 represents fish in post-absorptive resting conditions, excluding initial handling stress period,
231 and thus, we expect it to be close to the real SMR of the fish.

Setup of behavioral trials

The fish were allowed to recover from respirometry for at least four days before assayed for behavioral traits under chemical predator cues. They were not fed for 24-h prior to behavioral trials. The trials were conducted in custom-made mazes (Fig. 2) (size 400 mm wide × 1500 mm long, water depth 100 mm in the open area). During the trials, temperature in the maintenance tanks and test arenas was on average 5.0 ± SD 1.5°C. The rate of water flow was adjusted to ~8 L min^{-1} (~7.6–8.8 L min^{-1}) during the trials. This allowed for at minimum 1.26 times the arena volume of water to flow between consecutive trials, which was considered sufficient to minimize potential carry-over effects of chemical cues between trials. The arena was lit by LED lights (CRI90 LED chain in waterproof silicon tube, 3000-3300K, 4.8W m^2) situated along one long edge of the arena (>70 lux across the arena depending on the distance from the light source). Half-way across the arena was a brick gate situated next to one side, allowing entry from the other side. Behind the brick, natural pebbles (~3–5 cm in diameter) were scattered unevenly on the floor. One stone was provided for shelter and another was in the center of the arena in front of the start box (Fig. 2). Four structurally similar arenas were used in the experiment, but two of the arenas were mirror images of the other two with respect to the location of the gate.

Upstream from the flow-through test arena section was a section divided by a metal grid (5 mm mesh size) where a hatchery-reared burbot (*Lota lota*) (length ~30-40 cm) was placed to introduce chemical cues of a natural predator of juvenile brown trout. Burbot are nocturnal bottom-dwelling predators that are likely difficult for prey to detect visually, but their odor induces antipredator responses in prey species (Ylönen et al. 2007). Burbot were maintained by feeding them with pieces of various cyprinids and vendace (*Coregonus albula*) during

257 rearing, but fresh pieces of brown trout were used for two days prior to and every 2–3 days
258 during the trials (feeding occurred in separate tanks, not the behavioral arenas). Approx. 5g of
259 brown trout /meal was offered to the burbot, but not all pieces were eaten presumably due to
260 low temperature. Burbot (N = 8) were moved to the test arenas at least one day before the
261 trials and changed in each arena every 10–15 trials (2–3 days).
262
263 Before each trial, individual brown trout were haphazardly dip-netted from their rearing tanks
264 under red light and placed into black 10-L buckets filled with ~8L of water from the flow-
265 through system. Fish were identified by PIT tags and left undisturbed for 10 min before being
266 transferred into the start box located downstream from the test arena by pouring. During each
267 trial, the trout was acclimatized in the start box for 3 min, after which the door of the box was
268 opened by pulling a string from behind a curtain. The movements of the fish were recorded
269 from above using two CCTV infrared cameras (two arenas simultaneously filmed using the
270 same camera) for 10 min (of which the first 9 min 45 s was included in the behavior analysis).
271 The behavioral trial was repeated three times between 8:00 and 11:00 for each focal fish, with
272 an average time of 4.3 days (range 1–8 days) between consecutive trials. One trial from four
273 fish was omitted from the analysis due to error in data collection. The order in which batches
274 of four fish were captured on the same day from the same tank for the four arenas was
275 recorded (batch from hereon, levels 1–5, four individuals from batch 6/7 combined to batch
276 5).
277
278 *Testing behavioral responses to burbot*
279 To confirm that burbot odor was perceived as risky by the brown trout in the personality
280 assays, we studied the response of brown trout to burbot odor in a separate experiment using
281 individuals from wild HV (N = 9) and wild LV groups (N = 10). These fish were acclimated

282 in similar tanks as the personality-tested fish at 12h:12h L:D photoperiod for one week. The
283 behavior of each individual was tested on six different days in the presence and absence of
284 predator odor (3 trials in each condition in haphazard order). 3–4 different arenas were used
285 for each fish on different days to reduce fish habituation to a certain arena. All trials were
286 conducted between 14:40 and 17:00. Control treatment arenas were emptied and thoroughly
287 rinsed with pressurized tap water and water flow maintained for >2h before the trials to avoid
288 carry-over effects from burbot odor in previous trials (it was not possible to conduct the tests
289 prior to the experiment on the angling selection lines due to the limited time period with
290 stable water temperature in the hatchery). The water used in the flow-through system
291 originated from lake Kivesjärvi, where burbot is a common species; thus, dilute traces of
292 burbot odor may have been present throughout the study.
293
294 *Analysis of video recordings*
295 Behavioral data were collected from videos using manual tracking with AV Bio-Statistics 5.2
296 timing software. The observers were blind to the identity of fish in all recordings. Analyses
297 were conducted in haphazard order, and each trial was analyzed once. In total four people
298 analyzed the videos (JMP, NA, AL, SM). Four behaviors were characterized along the
299 "exploration" personality axis, as defined by Réale et al. (2007). That is, fish were in a new
300 environment during the tests and the odor of predator was previously unknown to the fish
301 given the fish had not experienced natural predation risk. The behavioral events timed from
302 the videos were 1) *latency* – the time from the start of the experiment until the whole body of
303 fish emerged from the start box, (after Boulton et al. 2014; Moran et al. 2016; Vainikka et al.
304 2016); 2) time until fish passed the gate to the upstream section of the arena (arrow in Fig. 2),
305 but this was not analyzed because of many fish not entering this section; instead we recorded
306 3) *exploration tendency* – a binary variable indicating whether the whole body of the fish

307 passed the gate within the arena; and 4) *exploration intensity* – the proportion of time spent
308 actively swimming after emerging from the start box. We used the proportion of time rather
309 than absolute time to reduce the dependence of activity from latency. Activity was thus
310 calculated as the total mobile time outside the box divided by total time outside the box. Fish
311 was considered immobile when not moving for longer than ~2 s.
312
313 **Sex determination from DNA samples**
314 To consider potential sex differences in the studied traits, we identified the sex of fish using
315 PCR amplification of the sexually dimorphic *sdY* locus, which identifies the correct sex in
316 brown trout with nearly 100% accuracy (Quéméré et al. 2014); details in Appendix A.
317
318 **Statistical analyses**
319 A principal component analysis (PCA) of behavioral data collected from the fish that emerged
320 from the box, i.e., data with no missing observations showed that eigenvalues were all < 1.5,
321 i.e., that the three variables were not strongly correlated (Fig. S1, Fig. S2). Therefore, each
322 behavioral variable was analyzed as separate response variable using univariate models
323 (Table 1 for sample sizes).
324
325 Variation in each response variable (SMR and behavioral variables) was explained with a
326 univariate model, including breeding group and acclimation conditions as explanatory terms
327 (Table 2). All analyses were conducted in R v.3.3.2 (R Core Team, 2016). Linear (LMM) and
328 generalized mixed-effects models (GLMM) were fitted using package *lme4* (Bates et al.
329 2015) with *lmerTest* (Kuznetsova et al. 2017) and the frailty models using package *coxme*
330 (Therneau, 2018). The data were visualized using ggplot2 (Wickham 2009). Statistical
331 significance was determined as $\alpha = 0.05$ in all models.

SMR and body mass were $\log_{10}$-transformed for the LMM to account for the scaling of metabolic rate with body mass. The models used for different behavioral variables were: 1) LMM for *exploration intensity*, where a higher value indicates higher proportion of time spent actively swimming, 2) a frailty model (i.e. mixed effect Cox proportional hazards models for time-to event data (Collett 2015)) for *latency*, where higher trait values and negative model coefficients indicate longer time to emergence, and 3) a GLMM for *exploration tendency* (Bernoulli-distribution), where entering or not entering the upstream sector was indicated by 1 and 0, respectively. Trial repeats were encoded as a continuous variable: -1, 0, and 1 in data from angling selection experiment and as 1–6 from burbot vs. control experiment. In 8 trials, the fish jumped out of the start box prior to the trial and their behavior was analyzed for 9 min 45 s min after the jump.

For LMMs and GLMM, the main effects of population, selection line, and photoperiod were separately tested using linear hypothesis testing (function *lht* in package *car*) using restricted models, where each respective main effect and its interactions were defined zero and compared to the full model using F-tests. From LMM and GLMM models, the estimated marginal means and confidence intervals were estimated with package *ggeffects* (Lüdecke 2018). All linear models were checked for homoscedasticity and normality of residuals. For all response variables, the effect of sex was analyzed in models including the fixed effect of sex as well as the effects from original models, except photoperiod or its interactions due to limited sample size with known sex. For further details see Appendix A, and Data accessibility.

To assess individual-level correlation among the behavioral variables and SMR, Pearson's product moment correlations were calculated between residuals from a linear model with $\log_{10}$ SMR as the response variable and $\log_{10}$ body mass in kg as the explanatory variable, and Best Linear Unbiased Predictors (BLUPs) for latency or exploration intensity. BLUPS were obtained from linear mixed models including only individual as random effect, and only for the trials where the fish emerged from the start box.

Results

SMR

The LMM indicated a significant effect of body mass and population on SMR, with fish from wild background having higher SMR than fish from the hatchery background, but no effect of selection line (Fig. 3, Table 3). Sex of fish had no effect on SMR ($F_{1, 58.215} = 0.067$, $P = 0.797$).

Behavior in angling selection lines

Fish emerged from the start box during the recorded time in ~84% of the trials. Mean latency for the fish that emerged was 1.83 min (range 0 – 9.54 min). There was a significant effect of angling selection ($P = 0.027$) and a slightly non-significant interaction effect ($P = 0.054$) of population background and angling selection on latency (Table 4). This was observed as an elevated risk to emerge in fish from LV background compared to HV background in the hatchery population, but not in the wild population (Fig. 4A).

Exploration intensity did not differ between populations or angling selection lines, but the fish spent less time exploring the arena after acclimation in constant light compared to the 12h light:12h dark photoperiod (Table 4). Mean exploration intensity was 0.37 (range 0.0015 – 1.0).

Angling selection had contrasting effects on exploration tendency in each population: in the hatchery population, a higher proportion of fish from LV selection line were explorative than from HV selection line, while there was an opposite tendency in the wild population (Fig. 4B; Table 4). In addition, exploration tendency increased with repeats of the behavioral trial.

Sex did not have a significant effect on any behavioral trait (female vs. male, Exploration intensity: $F_{1,39.612} = 1.217$, $P = 0.277$; Latency: $e^{coef} = 1.03$, $z = 0.29$, $P = 0.770$; Exploration tendency: $z = –0.514$, $P = 0.607$).

There was no correlation between mass-adjusted SMR and behavioral traits as assessed with initial, anti-conservative test using individual BLUPs (see Houslay & Wilson 2017) for neither exploration intensity (r = -0.006, $t = -0.05_{79}$, P = 0.96) nor latency (r = -0.083, $t = -0.75_{79}$, P = 0.46).

Behavioral responses to predator presence

The were no significant direct effects of predator cues on behavioral traits (Table 5). Repeating the behavior trials six times for each fish, three times with a burbot present and three times in control conditions, led to a significant decrease in exploration intensity with trial repeats (Table 5). The variance of exploration intensity between individuals appeared seemingly higher in the presence of burbot, but this was not significant in Levene's test of homogeneity of variance ($F_{1,93} = 0.214$, $P = 0.645$). Risk of emergence increased with increasing behavior trial repeats and between-individual variation in latency was high (~10% higher variance in burbot vs. control data compared to data from angling selection lines).

407 **Discussion**

408 We found that captured and non-captured brown trout produced offspring that differed in
409 exploration-related behaviors. Against our expectations, the LV selection line was more
410 explorative in a new environment than the HV line in the hatchery population. However, in
411 the wild population, there was no significant response to angling selection in exploration
412 measured as latency to emerge. However, we found a significantly contrasting response in the
413 likelihood of exploring the arena after emergence compared to the hatchery line, with the HV
414 line being more explorative than the LV line. The results broadly agree with behavioral
415 responses found in the offspring from the same angling selection experiment in their first
416 summer, although the performed personality assays differed between the two studies;
417 Alioravainen et al. (2020a) assayed fingerlings at warm temperatures in simple arenas without
418 predator cues. Together, these studies provide evidence for a heritable link between angling
419 vulnerability and exploratory behavior assessed in controlled settings but highlight that such
420 connections can be population or environment specific. The smaller differences in the
421 behavior between angling selection lines from the wild population than from the hatchery
422 population may result from several reasons. First, genetic variation in the wild population was
423 smaller than in the hatchery population (Lemopoulos et al. 2019a). Second, the parental wild
424 fish had no juvenile hatchery history, and they were captured directly from seminatural ponds
425 with a stream and a pool section during angling, while the hatchery fish were fished in a plain
426 concrete tank under high density, which may have introduced density-dependent behavioral
427 effects that were absent in the wild fish.

428

429 The result that mass-corrected SMR was higher in the offspring of wild fish than those from
430 hatchery parents was unexpected. The hatchery environment is expected to favor individuals
431 with a fast metabolic rate (Reid et al. 2012; Robertsen et al. 2018). However, because

metabolic rate measurements can induce stress responses (Murray et al. 2017) and domestication-related phenotypic changes can be evident in hatchery environments already after a single generation in salmonids (Christie et al. 2016, Islam et al. 2020), the result could be explained by a better ability of the hatchery-population fish to adjust to handling during metabolic rate measurements. Further, metabolic rate might relate to the life-history strategy of the fish (Rosenfeld et al. 2015), as the wild fish represented resident and the captive fish migratory brown trout forms (Lemopoulos et al. 2019b). The potential effects of angling selection on metabolic rate were smaller than the effects of population, and our technique lacked sensitivity to detect minor differences between groups, but this could be reassessed in further studies.

Differences in stress coping styles, i.e. sensitivity of the neuroendocrine stress responses (Schjolden et al. 2005; Koolhaas et al. 2010), could partly explain why the results on behaviors and SMR were partly contradicting our expectations. If the LV fish from the hatchery population were more reactive compared to the HV fish, their behavior may have indicated a higher stress response to the experiment and heightened escape behavior; this effect has also been suggested to occur in pike (*Esox lucius*) (Laskowski et al. 2016). Angling intensity itself can also influence the serotonergic and dopamine systems in fish (Koeck et al. 2018), and given that Koeck et al. (2018) found clear species differences in the effect between rainbow trout and brown trout, it can be speculated that population differences in how fish respond physiologically to disturbance caused by angling are also possible. Changes in stress-related physiological responses could explain which individuals are most vulnerable to angling. Relatedly, the most angling-vulnerable parent fish in the hatchery strain may have had the lowest status in the dominance hierarchy within the concrete ponds, and therefore been the hungriest and the most prone to attack the fly patterns. In contrast to the hatchery

457 population, wild fish were under more natural-like ponds during the angling trials and this
458 may have allowed to them to maintain more of their natural behavior, including hierarchy
459 related to feeding, and by extension, to attacking the flies.
460
461 It is likely that for both population and angling selection line differences that genetic
462 inheritance would explain our results at least partly; Ågren et al. (2019) showed that the
463 heritability in exploration-related principal component was 0.1 ± 0.065 SE in the same
464 hacthery strain of brown trout, along with hatchery-wild crossbred strains. In Kortet et al.
465 (2014), low heritabilities were reported for exploration and boldness -related personality axis,
466 but that of freezing tendency was 0.14, similar to Ågren et al (2019). In three-spined
467 stickleback (*Gasterosteus aculeatus*), behavioral traits related to exploration and boldness in
468 the presence and absence of predation risk were moderately heritable (Dingemanse et al.
469 2009). Importantly, angling vulnerability itself is heritable in largemouth bass (Philipp et al.
470 2009).
471
472 Photoperiod had no influence on the relative differences between populations or on the
473 absolute metabolic and behavioral traits, except on exploration intensity, which, however, was
474 not affected by population background or angling selection. This suggests that exploration
475 and metabolic rate differences between populations can be consistent across environments.
476 Constant light is not encountered by brown trout during the winter; hence the 24-hour light
477 regime could be considered unnatural and potentially stressful for the fish. Constant light can
478 disrupt entrainment of endogenous rhythms by inhibiting the synthesis of melatonin and by
479 directly affecting photosensitive proteins (Falcón et al. 2010; Peirson et al. 2009). In general,
480 non-tropical species are expected to be particularly sensitive to photoperiod disturbances due

481 to the role of day length in anticipating seasonal changes in environmental conditions
482 (Borniger et al. 2017).
483
484 The differences we found between populations can also be explained by the level of
485 domestication, as the hatchery stock had been reared in captivity for several generations.
486 Populations frequently differ in e.g., metabolic rate and behavioral syndromes (Dingemanse et
487 al. 2007; Lahti et al. 2002; Polverino et al. 2018), driven by environmental differences,
488 natural selection, founder effects, and genetic drift. The populations we studied also differed
489 in their life-histories, with the wild population being clearly less migratory than the hatchery
490 population (Lemopoulos et al. 2019b). Moreover, juveniles from the wild population show
491 lower tendency for post-release dispersal in a stream environment than juveniles from the
492 hatchery population (Alioravainen et al. 2020b). Although we reared offspring under common
493 garden conditions and maximized genetic diversity within each group through a fully factorial
494 breeding matrix, it is possible that differences in the early rearing environments of wild and
495 hatchery parents had contrasting effects on offspring through parental or epigenetic effects
496 (Crews et al. 2012; Reddon 2012). The duration of these effects on offspring physiology can
497 be short- or long-lasting (Bell et al. 2016; Metzger and Schulte 2016; Munday et al. 2017).
498
499 Our goal was to study exploration/risk-taking -related behaviors by subjecting fish to the
500 olfactory cues of a natural predator that had fed on conspecifics, which was expected to cause
501 a strong antipredator response (Vilhunen and Hirvonen 2003; Ferrari et al. 2010). Although
502 no direct effect of predator presence on brown trout behavior was found in this study, we
503 found a strong decline in the exploration intensity of fish with increasing predator/control trial
504 repeats, which could indicate the development of an antipredator response, evident as
505 increased hiding and decreased activity in juvenile salmonids (Vilhunen 2006; Vilhunen and

Hirvonen 2003; Kopack et al. 2015). However, we did not separate fish into control and predator exposure treatments, but each fish in the test served as their own control, and thus the effect may also be related to habituation into the test arenas. We conducted the test of predator cues only on the wild fish offspring, given that innate responses were expected to be stronger in this population, but notably none of the individuals in the behavior trials in this study had been exposed to predators before the trials, apart from potential traces of piscivore odors in the rearing water. It is therefore not surprising that results were not as strong as in previous studies using wild-caught individuals (Álvarez and Nicieza 2003). In our study, the scarcity of responses to the presence of predator odor, measured in the offspring of wild fish, indicate only weak innate responses. Nevertheless, the (non-significant) tendency for lower exploration intensity in the presence of burbot than in control conditions resembles previously shown antipredator responses in salmonids.

Conclusions

Our results suggest population-specific potential for rapid human-induced evolution in the behavior of a popular fishing target species. Population differences in the response to selection may have arisen from contrasting dependence of angling vulnerability from fish behavior, or from differences in the heritability of selected behaviors. This highlights the complexity of ecological and innate factors that can contribute to angling-induced selection in natural populations. Overall, the results from this common garden experiment suggest a significant genetic effect upon the behavior of brown trout parr.

Conflict of Interest

The authors declare that they have no conflict of interest.

Data accessibility

All data and R codes for analyzing respirometry data and for the statistical models are available in GitHub (https://github.com/jprokkola/Strutta_repo). Data will additionally be made available in a permanent repository upon acceptance for publication. Videos of behavior trials will be made publicly available in Figshare (accession) upon acceptance for publication.

Appendices

Appendix A. Supplemental material and methods.

Author contributions

A.V. and P.H. produced the selection lines, J.M.P, N.A. and A.V. designed the experiment, J.M.P., N.A., S.M. and A.L. collected the data, J.M.P. and L.M. analyzed the data, J.M.P. wrote the initial draft of the manuscript. All authors contributed to preparing the manuscript.

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804 Tables

805 Table 1. The number of individuals in each group in each analysis, mass-specific SMR values, and fish total body length and mass (mean ± SD)

806 at the end of the experiment. (HV = high, LV = low vulnerability)

807

Photoperiod	Population	Selection line	N (metabolic rate)	N (latency, exploration tendency & intensity)	N (body size)	N males / females (unknown)	Body length / mm	Body mass / g	SMR mg O_2/L /kg/h
12:12	Hatchery	HV	15	15	14	9 / 5 (1)	117 ± 10	17.1 ± 4.3	260.7 ± 65.5
		LV	10	14	14	6 / 2 (7)	115 ± 13	16.5 ± 6.7	300.4 ± 16.5
	Wild	HV	13	14	14	6 / 6 (3)	117 ± 7	17.4 ± 3.2	261.9 ± 41.7
		LV	15	15	14	7 / 7 (1)	115 ± 9	16.6 ± 4.3	268.8 ± 49.5
24	Hatchery	HV	9	10	9	6 / 3 (1)	119 ± 9	17.7 ± 4.7	261.2 ± 36.0
		LV	7	10	6	0 / 4 (6)	124 ± 9	19.6 ± 3.9	299.4 ± 59.4
	Wild	HV	8	10	6	2 / 3 (5)	116 ± 9	17.8 ± 7.1	260.9 ± 55.3
		LV	6	10	5	2 / 1 (7)	119 ± 9	17.8 ± 3.0	305.2 ± 71.8

Table 2. The main statistical models used in this study. Abbreviations explained below the table.

Study section	Response variable	Model
I. Angling selection experiment	$Log_{10}(SMR)$	$y_{ij} = \beta_0 + \beta_1 PHO_{ij} + \beta_2 POP_{ij} + \beta_3 SEL_{ij} + \beta_4 POP_{ij} \times SEL_{ij} + \beta_5 POP_{ij} \times PHO_{ij} + \beta_7 logBM_{ij} + \beta_8 WT_{ij} + p_l + e_{ij}$
	Exploration intensity	$y_{ijk} = \beta_0 + \beta_1 PHO_{ijk} + \beta_2 POP_{ijk} + \beta_3 SEL_{ijk} + \beta_4 POP_{ijk} \times SEL_{ijk} + \beta_5 POP_{ijk} \times PHO_{ijk} + \beta_6 REP_{ijk} + b_i + c_j + d_k + e_{ijk}$
	Latency	$\lambda(t) = \lambda_0(t) e^{\beta_1 PHO_{ijk} + \beta_2 POP_{ijk} + \beta_3 SEL_{ijk} + \beta_4 POP_{ijk} \times SEL_{ijk} + \beta_5 POP_{ijk} \times PHO_{ijk} + \beta_6 REP_{ijk} + b_i + c_j + d_k}$
	Exploration tendency (1 = explorative, 0 = un-explorative)	$y_{ij} \sim Bernoulli(p_{ijk})$ $logit(p_{ijk}) = \beta_0 + \beta_1 PHO_{ijk} + \beta_2 POP_{ijk} + \beta_3 SEL_{ijk} + \beta_4 POP_{ijk} \times SEL_{ijk} + \beta_5 POP_{ijk} \times PHO_{ijk} + \beta_6 REP_{ijk} + b_i + c_j + d_k$
II. Behavioral responses to burbot olfactory cues	Exploration intensity	$y_{ijk} = \beta_0 + \beta_1 SEL_{ijk} + \beta_2 TRE_{ijk} + \beta_3 REP_{ijk} + \beta_4 BL_{ijk} + b_i^{(1)} CON + b_i^{(2)} BUR + c_j + d_k + e_{ijk}$
	Latency	$\lambda(t) = \lambda_0(t)\, e^{\beta_1 SEL_{ijk} + \beta_2 TRE_{ijk} + \beta_3 REP_{ijk} + \beta_4 BL_{ijk} + b_i + c_j + d_k}$
	Exploration tendency	$y_{ijk} \sim Bernoulli(p_{ijk})$ $logit(p_{ijk}) = \beta_0 + \beta_1 SEL_{ijk} + \beta_2 GR_{ijk} + \beta_3 REP_{ijk} + b_i + c_j + d_k$

β_0 Intercept, *PHO* Photoperiod, *POP* Population, *SEL* Selection, *logBM* Log_{10} body mass in kg, *WT* Water temperature in °C, *BL* Body length in mm – mean (118.8182 mm for I, 122.4464 mm for II), *REP* Trial repeat, *TRE* Treatment, p_l the random effect for chamber l, b_i random effect for fish i, c_j the random effect for arena j, d_k the random effect for batch k, *e* Residual, λ_0 baseline hazard, *t* time, *CON / BUR* binary explanatory variables for burbot and control treatments.

811 Table 3. Results from model for SMR. The zero levels for contrasts were: photoperiod 12:12,
812 population hatchery, and selection line HV. F and P- values for the interactions and
813 temperature effect were obtained from Type III sums of squares and Satterthwaite
814 approximation for degrees of freedom. For the other fixed effects, linear hypothesis tests
815 using F-test on restricted models with each main effect and its interactions set to zero were
816 used – residual degrees of freedom are given for these tests. Significant ($P < 0.05$) effects
817 shown in bold. For the intercept, t-test value is shown.

Fixed effects	Estimate ± SE	Num df	Res / Den df	F	P
Intercept	0.97 ± 0.20	1	74.522	4.96 (t)	<0.001
Photoperiod	0.004 ± 0.02	2	72.09	0.41	0.664
Population	**0.051 ± 0.02**	**3**	**73.355**	**2.78**	**0.047**
Selection	0.031 ± 0.02	2	72.281	1.27	0.286
Temperature	0.02 ± 0.02	1	73.866	1.32	0.254
Log_{10} body mass	**0.27 ± 0.09**	**1**	**72.773**	**9.90**	**0.0024**
Pop × selection	-0.031 ± 0.03	1	72.173	1.342	0.250
Pop × photoperiod	0.014 ± 0.03	1	72.119	0.241	0.625
Random effects	**Variance (SD^2)**				
Chamber	0.039^2				
Residual	0.060^2				

Table 4. Results of models for behavior traits in brown trout from hatchery and wild populations and two angling selection lines (HV and LV). The zero levels for contrasts in all models were: photoperiod 12:12, population hatchery, and selection line HV. For model equations, see Table 2. For exploration intensity, F- and P-values for the interactions and trial repeat were obtained from Type III test, and for the other main effects from linear hypothesis tests using restricted models with each main effect and its interactions set to zero. For latency, proportional hazard estimates for risk or emergence (± standard error) are shown with hazard ratios (e^{coef}). For latency and exploration tendency, Wald Chisquare test was used to determine significance of fixed effects. Fixed effects with $P < 0.05$ shown in bold. For intercepts, t- or z-test values shown.

	Fixed effects	Estimate ± SE	Num Df	Res/Den Df	F	P
Exploration intensity (LMM)	**Intercept**	**0.30 ± 0.04**	**1**	**33.18**	**7.78 (t)**	**<0.001**
	Photoperiod	**-0.75 ± 0.04**	**3**	**84.03**	**6.53**	**0.001**
	Population	0.08 ± 0.06	3	42.50	1.40	0.242
	Selection	-0.01 ± 0.04	2	74.67	0.10	0.903
	Pop × selection	0.025 ± 0.06	1	197.41	1.28	0.259
	Photoperiod × pop	-0.070 ± 0.06	1	81.43	1.37	0.245
	Trial repeat	-0.017 ± 0.02	1	44.24	0.20	0.655
	Random effects	**Variance (SD^2)**				
	ID	0.054^2				
	Batch	0.036^2				
	Arena	0.016^2				

	Fixed effects	Coef	e^{coef}	SE	z	P
Latency (frailty model)	Photoperiod	0.13	1.14	0.26	0.49	0.630
	Population	-0.083	0.92	0.30	-0.27	0.780
	Selection	**0.57**	**1.76**	**0.26**	**2.21**	**0.027**
	Pop × selection	-0.71	0.49	0.37	-1.92	0.054
	Photoperiod × pop	-0.060	0.94	0.38	-0.16	0.870
	Trial repeat	**0.23**	**1.26**	**0.082**	**2.83**	**0.005**
	Random effects	**Variance (SD^2)**				
	ID	0.625^2				
	Batch	0.079^2				
	Arena	0.097^2				

	Fixed effects	Estimate ± SE	Wald χ^2	Df	P
Exploration tendency (GLMM)	Intercept	0.55 ± 0.63	0.88 (z)	1	0.380
	Photoperiod	-0.63 ± 0.63	1.80	1	0.179
	Population	1.07 ± 0.72	0.058	1	0.810
	Selection	1.54 ± 0.64	0.43	1	0.511
	Pop × selection	**-2.46 ± 0.92**	**7.18**	**1**	**0.007**
	Photoperiod × pop	0.07 ± 0.88	0.006	1	0.936
	Trial repeat	**0.58 ± 0.21**	**7.79**	**1**	**0.005**
	Random effects	**Variance (SD^2)**			
	ID	1.398^2			
	Batch	0.270^2			
	Arena	0.762^2			

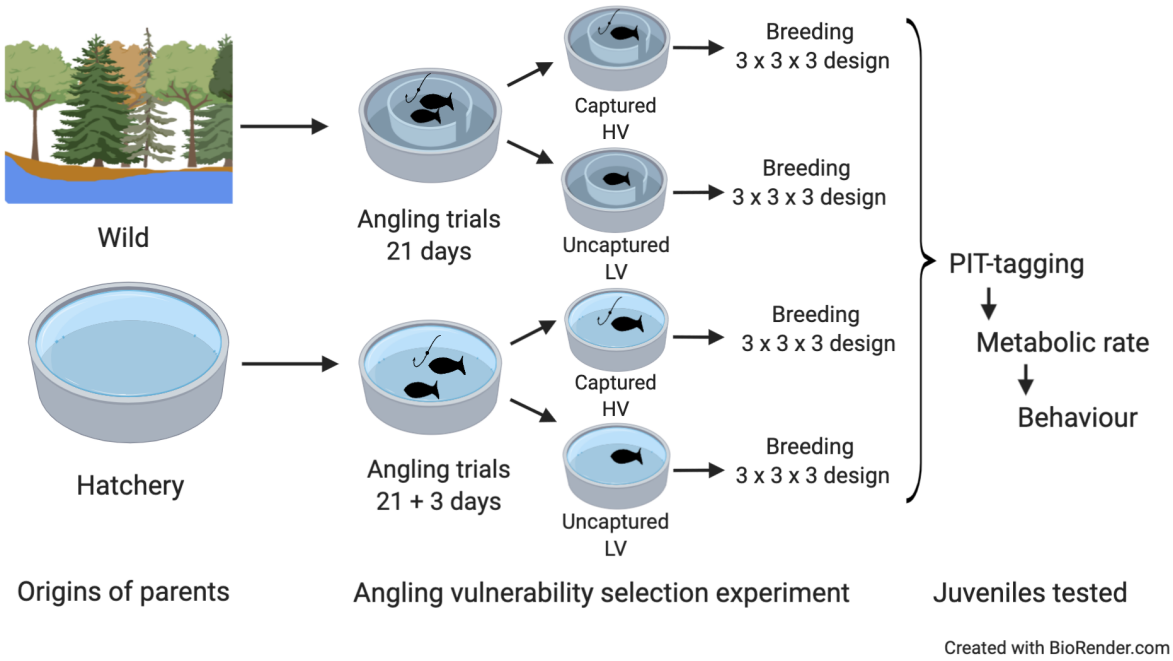
832 Table 5. Results of models for behavioral traits in the presence of predatory olfactory cues
833 and control conditions in brown trout. For exploration intensity, the t-test was used with
834 Satterthwaite approximations to degrees of freedom and the model was fit with restricted
835 maximum likelihood. For latency, proportional hazard estimates for risk or emergence
836 (± standard error) are shown with hazard ratios (e^{coef}). For latency and exploration tendency,
837 Wald Chisquare test was used to determine significance of fixed effects. The zero levels for
838 contrasts in all models were: treatment control and selection line HV. Significant effects ($P <$
839 0.05) shown in bold.

	Fixed effects	**Estimate ± SE**	**Den Df**	**t**	**P**
Exploration intensity (LMM)	**Intercept**	**0.435 ± 0.060**	**23.25**	**7.198**	**<0.001**
	Selection line	0.012 ± 0.065	9.59	0.18	0.861
	Treatment	-0.081 ± 0.042	15.85	-1.928	0.072
	Trial repeat	**-0.029 ± 0.010**	**71.62**	**-2.97**	**0.004**
	Body length	-0.00009 ± 0.004	8.63	-0.02	0.984
	Random effects	**Variance (SD^2)**			
	ID (burbot)	0.122^2			
	ID (control)	0.077^2			
	Batch	0.000			
	Arena	0.000			
	Residual	1.400^2			
Latency (frailty model)	**Fixed effects**	**Coef ± SE**	**e^{coef}**	**z**	**P**
	Selection line	0.336 ± 0.372	1.399	0.900	0.370
	Treatment	0.089 ± 0.220	1.093	0.400	0.690
	Trial repeat	0.113 ± 0.065	1.120	1.759	0.080
	Body length	-0.006 ± 0.026	0.994	-0.230	0.820
	Random effects	**Variance (SD^2)**			
	ID	0.661^2			
	Batch	0.210^2			
	Arena	0.080^2			
Exploration tendency (GLMM)	**Fixed effects**	**Estimate ± SE**	**z**	**P**	
	Intercept	1.449 ± 0.801	1.808	0.0706	
	Selection line	0.659 ± 0.724	0.910	0.363	
	Treatment	-0.63 ± 0.487	-1.294	0.196	
	Trial repeat	-0.066 ± 0.142	-0.465	0.642	
	Random effects	**Variance (SD^2)**			

ID	1.140^2
Batch	0.000
Arena	$(1.847 \times 10^{-5})^2$

842 **Figures**

843



844

845 Fig. 1. A diagram of the experimental design. Parental fish were placed in size-assortative

846 ponds (N = 64 and 167 for large- and small-size fish in hatchery population, and N = 53 and

847 91 in the large- and small-size wild fish, respectively) before angling. After 21 days of

848 angling, or after the first capture, fish were transferred to two tanks similar to those used in

849 the angling trials. The hatchery stock individuals were thereafter fished for a second time (3

850 days of angling). Before breeding, fish were again combined in population-specific size-

851 assortative ponds (not shown in diagram). Further details in Alioravainen et al. (2020a).

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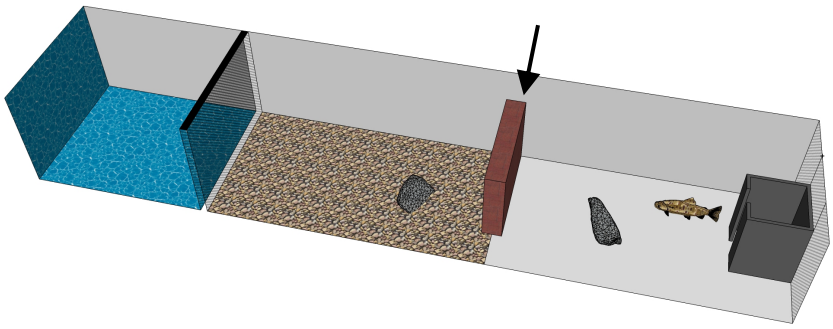

Fig. 2. A 3D-illustration of the arena used in personality trials without the left side wall. Water flow direction is left-right. Burbot was placed in the area indicated by blue color, upstream from the net (inaccessible to the brown trout). Pebbles were scattered in the brown-colored area. The grey box indicates the start box, where the fish was placed before the start of a trial. Latency was measured as time to emerge from the box. Exploration intensity was measured as swimming activity outside the start box arena after emergence. Exploration tendency was measured as whether or not the whole body of fish passed the gate indicated by an arrow.

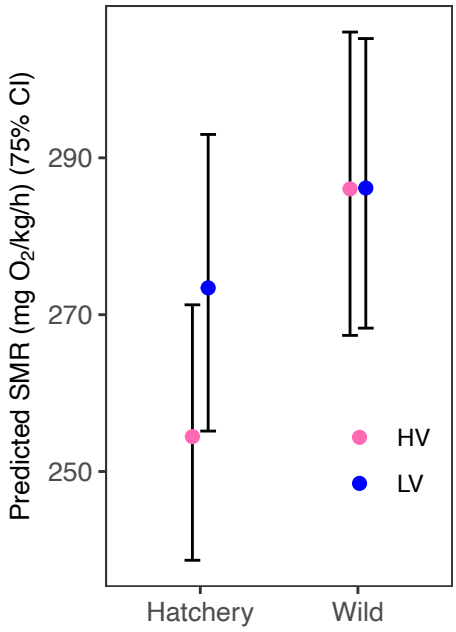

Fig. 3. Predicted SMR (estimated marginal means) across two populations and angling selection lines (HV – high vulnerability, LV - low vulnerability) in brown trout. Data from two photoperiods combined. Estimates and 75% confidence intervals were obtained from a linear mixed model and conditioned on fish average body mass and average temperature during measurements, back-transformed to linear scale and divided by average body size in kg to obtain mg $O_2kg^{-1}h^{-1}$. For N in each group, see Table 1.

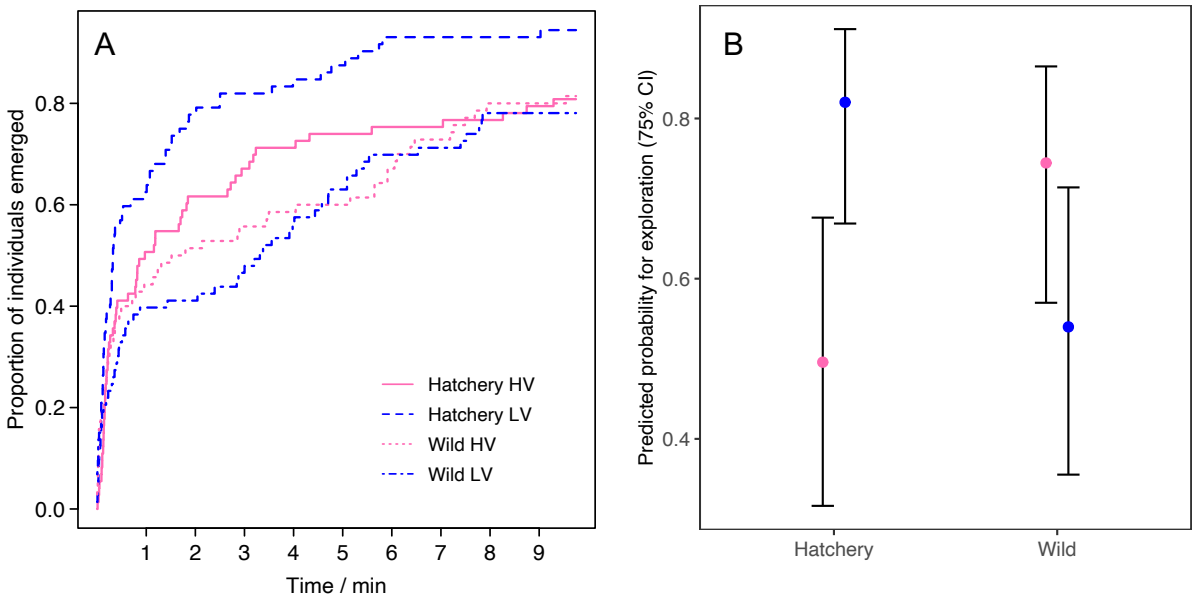

Fig. 4. Behavioral differences between two angling vulnerability selection lines (HV – high vulnerability, LV – low vulnerability) within the hatchery and wild populations. Data from photoperiods combined for clarity. A) Curves showing the proportion of individuals emerged from the start box, drawn with Kaplan-Meier estimator. B) Predicted exploration tendency (estimated marginal means) from GLMM with 75% confidence intervals for predicted values. Angling selection had opposing effects on exploration tendency in the two populations (Table 4). Predictions were made for the first trial repeat. For N in each group, see Table 1. Pink = HV, blue = LV.