Does boldness explain vulnerability to angling in Eurasian perch

*Perca fluviatilis*?

Anssi VAINIKKA1*, Ilkka TAMMELA1, Pekka HYVÄRINEN2

1Department of Biology, University of Eastern Finland, P.O. Box 111, FI 80101 Joensuu, Finland

2Natural Resource Institute Finland, Manamansalonantie 90, 88300 Paltamo, Finland

Abstract Consistent individual differences (CIDs) in behaviour are of interest to both basic and applied research, because any selection acting on them could induce evolution of animal behaviour. It has been suggested that CIDs in the behaviour of fish might explain individual differences in vulnerability to fishing. If so, fishing could impose selection on fish behaviour. In this study, we assessed boldness-indicating behaviours of Eurasian perch (*Perca fluviatilis*) using individually conducted experiments measuring the time taken to explore a novel arena containing predator (burbot, *Lota lota*) cues. We studied if individual differences in boldness would explain vulnerability of individually tagged perch to experimental angling in outdoor ponds, or if fishing would impose selection on boldness-indicating behaviour. Perch expressed repeatable individual differences in boldness-indicating behaviour but the individual boldness-score (the first principal component) obtained using principal component analysis combining all the measured behavioural responses did not explain vulnerability to experimental angling. Instead, large body size appeared as the only statistically significant predictor of capture probability. Our results suggest that angling is selective for large size, but not always selective for high boldness [Current Zoology 62 ( ) : – , 2016 ].

Keywords Behaviour, Fishing-induced evolution, Fishing vulnerability, Growth, Personality, Selection

Most animals including fishes display temporally consistent behavioural differences (CIDs) among individuals (Dall et al., 2004; Réale et al., 2007; Kortet et al., 2010; Stamps and Groothuis, 2010). CIDs in behaviour have been observed, for example, in individual tendency to explore novel environments, tendency to aggressive encounters, dispersal rate, vulnerability to predation or even in the risk of becoming fished (Wilson et al., 2011; Rasmussen and Belk, 2012; Härkönen et al., 2014; Mittelbach et al., 2014; Johnson et al. 2015). Personality traits, i.e. traits that underlie observable behavioural variation, are not only expressed consistently over relatively long periods in individual’s life, but may also be significantly heritable (Brown et al., 2007; Conrad et al., 2011; Kortet et al., 2014). Individual fish have been observed to differ in vulnerability to become captured by angling, even heritably (e.g. Tsuboi and Morita, 2004; Askey et al., 2006; Philipp et al., 2009). Vulnerability to angling is not a biologically meaningful personality trait *per se* (in natural conditions without fishing) but rather reflects variation in other personality traits such as boldness, exploration tendency or aggressiveness (Lewin et al., 2006; Biro and Post, 2008; Wilson et al., 2011). Therefore, the question

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* Corresponding author. E-mail: anssi.vainikka@uef.fi

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becomes which personality traits are the most important in affecting individual catchability (Wilson et al., 2011; Mittelbach et al., 2014).

CIDs in behaviour can affect individual vulnerability of a fish to become captured by angling (Klefoth et al., 2013), gill-netting (Biro and Post, 2008) or fly-fishing (Härkönen et al., 2014). Fish captured with different gears or in different habitats may also express comparatively different behavioural types (Wilson et al., 1993; Wilson et al., 2011; Härkönen et al., 2015). However, not all studies have found covariation between the CIDs in behaviour and vulnerability to fishing (Binder et al., 2012) or relative vulnerability to different fishing gears (Kekäläinen et al., 2014). Therefore, studies resolving how vulnerability to angling is related to traditionally defined dimensions of animal personality are needed. Individual differences in vulnerability to fishing can also result from experiential factors (Klefoth et al., 2013). Fish learn to avoid hooked baits (Beukemaj, 1970; Askey et al., 2006) and also fish personality may develop through experience and social interactions (Hellström and Magnhagen, 2011; Härkönen et al. 2014).

Popularity of recreational fisheries is increasing almost globally with the consequence that the effects of fishing become more and more affected by interactions occurring between the fish and the anglers (Post et al., 2002; Lewin et al., 2006; Post et al., 2008). Individual catchability differences could induce bias in any fish sampling procedure, and thus also contest the validity of many fish stock assessment practises (c.f. Olsen et al., 2012). In addition, if individual behavioural differences had a heritable basis, non-random mortality among behavioural types might induce evolution of animal personality or catchability through selection (Philipp et al., 2009). Since personality traits that may explain vulnerability to fishing are often coupled with important life-history traits such as growth rate (Biro and Stamps, 2008; Mittelbach et al., 2014), management implications of fisheries selection on fish behaviour are potentially severe and therefore require attention (Usi-Heikkilä et al., 2008).

Eurasian perch *Perca fluviatilis* is a commercially exploited freshwater fish in Europe and a target of extensive recreational angling and other fishing (Vainikka et al., 2012). Eurasian perch has been an important model species in comparative studies of life-history variation and behavioural ecology (e.g. Westerberg et al., 2004; Heibo and Magnhagen, 2005; Heibo et al., 2005). Perch show individually consistent behavioural differences that are impacted but not overwhelmed by social effects in groups (Magnhagen and Bunnefeld, 2009; Kekäläinen et al., 2014).

The principal aim of this study was to test if individually assessed boldness of Eurasian perch could explain individual’s vulnerability to experimental angling, and whether the link between boldness and vulnerability to angling would depend on the origin of the fish. As a secondary aim, the potential for angling-induced selection was examined by comparing the traits of fish that we captured or were not captured in the standardized angling trials. It was hypothesized that fish with high boldness and large size would be more vulnerable to angling than shy and small fish. Fish with large body size were expected to be more vulnerable to angling than small fish because of the predicted positive correlation between growth rate and boldness (Biro and Post, 2008), potential positive correlation between body size and boldness (Vainikka et al., 2012) and potential size-based dominance in feeding hierarchy (Koebele, 1985; Forrester, 1991).

1 Materials and Methods

1.1 Fish

To increase variance among fish and thus our potential to find general links among behaviour, life-history traits and vulnerability to angling, we used perch (*n* = 117) from three sources (Table 1). Most of the fish were collected from four emptied concrete aquaculture ponds (size 50 m²) of Kainuu Fisheries Research station (www.kfrs.fi) of Natural
Resources Institute Finland (64.404428 °N 27.5169603 °E) to which they had accidently arrived along with the incoming water from upstream Lake Kivesjärvi (64.4081984 °N 27.5038738 °E) at unknown time. These “pond fish” had been feeding on drifting food items coming with the water inflow and experienced a presence of in total 34 juvenile salmon or trout (120–250 mm in total length) while in the ponds. These fish were assumed naive to fishing, because there is no catch & release angling for perch in Lake Kivesjärvi and the intensity of angling is generally low (authors’ personal experience). In addition to the pond fish, fish collected from the wild were used. Lake Kivesjärvi fish (Table 1) were angled using artificial soft and crank baits on 27th–29th June 2012, and Lake Kangasjärvi (64.3916552 °N 27.4310726 °E) fish were angled in Lake Kangasjärvi (connected with the Lake Kivesjärvi through a brook) using mainly natural baits on 28th–29th of June 2012. Even though all the wild-collected fish were already captured by angling i.e. were vulnerable to fishing in an absolute sense, they were assumed to show relative, individual differences in a secondary angling attempt.

All the wild fish were individually tagged with 12 mm HDX PIT-tags (Texas Instruments Corp., USA) under anesthesia (with ethyl aminobenzoate “bentzocaine” solution in concentration 0.04 g l⁻¹) straight after the capture. The generally smaller pond-collected fish were tagged individually with 7 mm FDX PIT-tags (Loligo Systems, Denmark) between 7th and 18th September 2012. Prior to the experiments, the fish of wild origin were held in a 15 m² indoor fiberglass tank and the pond fish in three 3.2 m² fiberglass tanks so that fish smaller and larger than 140 mm in total length were kept in separate tanks. All perch were fed twice a week with frozen brown trout Salmo trutta fry, frozen small vendace Coregonus albula and commercially raised earthworms Dendrobaena veneta. Light rhythm (illumination intensity 8 lux) and water temperature followed the natural changes in the study area. Oxygen concentration stayed close to full saturation during the experiments (> 90%). Natural mortality attributed mainly to fish diseases was observed among wild-caught fish (Lake Kangasjärvi fish: 43.5 %, Lake Kivesjärvi fish: 39.3%) during summer, but at the time of the experiments, all fish were healthy.

1.2 Boldness assays

Boldness trials in the presence of a live predator (862 g burbot, Lota lota) upstream from focal fish were conducted in 1,890 mm × 390 mm × mm arena (Fig. 1) between 19th of September 2012 and 21st of October 2012 (Fig. 1). The arena contained a start tube, two shelter areas (with stones or plastic plants) and an open space between the shelter areas. The behavioural tests were conducted between 7:30 and 23:00. The upstream predator section was separated from the arena by a wire net (mesh size 10 mm). The arena was floored with sand and gravel (thickness varied between 150 and 350 mm because the start tube had to be placed close to the surface) so that the average water depth was 260 mm. The water current through the arena was kept constant at 10 l min⁻¹. Water temperature was decreasing during the experiments and varied between 5.6–11.9 °C. Water oxygen concentration varied between 9.4 - 10.3 mg l⁻¹. Based on preliminary experiments that aimed to optimize environmental conditions for maximal perch activity, illumination in the test area was set to be 1 lux (measured 5 cm above water surface).

All the pond-collected fish (n = 67) were tested twice between 19th September 2012 and 11th October 2012 in 1–20 day intervals, whereas the wild-collected fish (n = 50) were tested only once (due to logistic constraints) between 19th September and 21st October. No effort was invested to standardize the time between the two tests in order to study if the consistency of behaviour changes over time. In each test, the focal fish was first haphazardly dip-netted from the holding tank, transferred to the experimental arena in a 10 l plastic bucket and placed in the plastic dark green start tube (total length 290 mm, effective inner length 255 mm, diameter 200 mm), which was closed with a plastic door that was attached to a thin rope used to remove the door from a distance. After closing the fish into the start tube, the fish was let...
to acclimatize for 5 minutes before the door was remotely opened and fish behaviours were observed using a digital video system for 20 min. Two monochrome infrared cameras were used at 900 mm height from the water surface. Using time taking computer software (AV Bio-Statistics 4.9 by A.V.) the following responses were recorded in real time: 1) the time until the focal perch came out from the start tube, 2) the time until the fish reached the stones placed outside the start tube, 3) the time until the fish reached the plain bottom area (assumed potentially dangerous), 4) the time until the fish reached the plastic plants placed next to the predator section and 5) the time until the fish reached the metal grid next to the predator. If the fish did not reach certain point in arena, the response was assigned the maximum length of the experiment (20 min). Also the total number of events in each trial was counted, and the event times were used to calculate the total times spent in each section. In addition, total count of freezing events (clear immobility for at least a second) and their total span (in seconds) were recorded.

After the behavioural experiments, fish were anaesthetized (see above), measured for length and body mass, and returned to a 3.2 m$^2$ fiberglass holding tank to wait for the second trial or transferred to the outdoor angling ponds (see below). All the behavioural experiments were performed by a single person (I.T.).

1.3 Fishing trials

Directly after the last behavioural test on 11$^{\text{th}}$–21$^{\text{st}}$ of October 2012, the fish were randomly divided into two similar, rectangular 400 m$^2$ outdoor ponds with gravel bottom (depth ca. 2.0 m). The outdoor ponds supported natural zoobenthos. In addition, the incoming water from the Lake Kivesjärvi contained zooplankton (see Rodewald et al., 2011) and small fish. Three angling trials per day (fishing effort, $f = 1$ h per pond at once, trials in the morning at 8-10, noon 10-12 and afternoon 12–14) were conducted during four consecutive days between 30$^{\text{th}}$ of October 2012 and 3$^{\text{rd}}$ of November 2012. Water temperature during the angling trials was 3–5 °C. Final effort of one hour per pond was invested in the morning of 4$^{\text{th}}$ of November 2012. Rod (7 m, Geodet 200, Julia Rod, Italy), hook (Kamasan B525 eyed whisker barb, size #12, #14 or #16), 2 g float (Milo, Italy), monofilament fishing line (Stroft GTM, Germany, diameter 0.14 mm), weighting of the float to the minimal possible buoyancy and bait (a single red or white-coloured commercially raised blowfly larva) were standardized. Differently sized hooks were used to make it possible to catch fish of all potential sizes, but in general perch has a relatively large mouth and even perch of 60–70 mm in total body length can be captured with size #14 hook (authors’ personal experience). With the used high quality hooks loosing fish that has ingested the bait is rare and was not recorded in this study. Pond that was fished first at each angling occasion was randomized together with the bait colour and hook size. Equal effort was spent in each side of the pond to fish equally the whole surface area. At each capture, the fish was identified by PIT-tag code and released back to the original pond. After the fishing trials, the ponds were dried and all the fish were recovered for the measurement of body length and mass in anesthesia (as above). Based on the trials, the fish were classified as either 1) being vulnerable to angling (captured at least once) or 2) not being vulnerable to angling (not captured at all). In total four fish were found dead (cause unknown) in the outdoor ponds used for angling trials and were therefore excluded from the statistical tests. All the fishing trials were performed by the same person (I.T.).

Adjusted Fulton’s condition factor, $K$, was calculated for each individual at both size measurement events using the equation, $K = \frac{100 g}{\text{cm}^3} \times \text{total body mass (g) (total body length (cm))}^b$, where $b$ (3.15355) was obtained as the slope of a regression of ln(weight) on ln(total length) using all the data pooled from the measurements (linear regression, $R^2 = 0.941, n = 232, P < 0.001$, Bolger and Connolly, 1989).
1.4 Data analysis

Ln-transformed (in order to meet normality) behavioural data were first studied for repeatability using interclass correlation coefficient of individual recorded variables (Lessells and Boag, 1987). All variables showing positive repeatability except for section times other than the time spent among artificial plants next to the predator were entered into a principal component analysis (Table 2) used to derive a combined factor score of boldness with regression method (see also Kekäläinen et al., 2014). Most section times were excluded from the analysis due to their very low repeatability (Table 2). Environmentally induced variation was then removed from the resulting boldness score (principal component scores multiplied with -1) using a linear mixed effect model with a diagonal covariance structure for repeated measures. Population of origin, day of behavioural test (as day number from 1.1.2012), time of behavioural test (as minutes from 00:00) and water temperature were entered as fixed factors and individual intercept as a random factor. Additional models with additional fixed factors repeat, final fish length and final fish condition were fitted to examine their potential impact on individual boldness. The residuals of the mixed effect model represent individual intercepts of behavioural reaction norm (Dingemanse et al., 2009; Niemelä et al., 2013) and as such measures of individual boldness independently of the controlled environmental variables. Because alternative random intercept and random slope model had higher AIC than the used random intercept model and there was no general change in the boldness score between the first and the second trial, the slope was assumed zero (no plasticity in static experimental setting). For the twice-tested pond fish an average (still representing reaction norm intercept) of the two residual values was used. Residual boldness scores (or their average) were used to predict individual’s vulnerability to angling within and across different groups of origin. To examine if the consistency of behaviour would be dependent on the time between the two repetitive boldness trials, an absolute value of the difference between the first and the second boldness score was calculated and correlated with the number of days between the experiments using Pearson’s correlation.

Logistic regression analysis with backward stepwise elimination of non-significant variables (based on log-likelihood ratio testing) was used to examine which of the measured variables (residual boldness score, condition factor before and after the angling trials, length before the angling trials and origin of fish) explained vulnerability to angling (caught or not). The analysis was first run on the whole dataset, and then without the source of origin for each group of fish separately. T-test for independent samples with appropriate correction for heteroscedastic variances was used to compare the traits of captured and non-captured fish within and across different origins. Experimental ponds were assumed similar and their potential effects were not modelled in order to save degrees of freedom. The statistical tests were performed in IBM SPSS 21.0 for Windows (IBM Inc., USA), R 3.0.0 (The R Foundation for Statistical Computing) and in AV Bio-Statistics 4.9 program (by A.V).

2 Results

2.1 Behavioural variation and its repeatability

In two thirds of the trials (66.3 %), the focal fish left the start tube. The average time for leaving the start tube was 8.5 minutes for all the fish. On average, the fish spent 3.3 minutes among the plastic plants close to the predator section. Freezing behaviour was common; the average freezing time was 5.2 minutes.

Principal component analysis revealed that all the determined behavioural variables could be described effectively by a single principal component (Table 2) that accounted for 73.2 % of the total variance in behaviour (eigenvalue 3.19). The second component (eigenvalue 0.422) explained 10.5 %, the third component (eigenvalue 0.261) explained 6.5 % and the last (4.) component (eigenvalue 0.132) explained 3.3 % of the remaining variance. To ease the interpretation,
the principal component scores were multiplied with -1 to represent boldness instead of shyness. Therefore, high boldness score means fast exploration through the experimental arena and relatively long time use in the arena section closest to the live predator (Table 2). The boldness-score was individually repeatable (only pond fish: \( R = 0.227, 95 \% C.I. -0.001–0.455, n = 67 \)).

Linear mixed effect model revealed that boldness score varied with respect to fish origin (\( F_{2,136.78} = 18.93, P < 0.001 \)) and marginally along the behavioural testing date (\( F_{1,168.13} = 3.475, p = 0.064 \)) so that boldness increased in later tests. Water temperature (\( F_{1,167.78} = 1.502, p = 0.222 \)) and time of the behavioural test within a day (\( F_{1,153.41} = 0.081, P = 0.776 \)) did not significantly explain behavioural variation, and the formed residual boldness score was completely independent of water temperature (Pearson’s \( R = -0.003, n = 183, P = 0.967 \)). According to Bonferroni pairwise statistics, fish collected from aquaculture ponds were bolder (estimated marginal mean 0.409) than the fish from the wild, but the Lake Kangasjärvi (estimated marginal mean -0.922) and Lake Kivesjärvi (estimated marginal mean -1.346) fish did not differ from each other in boldness. There was no difference in the first and the second behavioural test (when repeat included as factor in the abovementioned model, the effect for it: \( F_{1,126.11} = 0.002, P = 0.965 \)). When fish length and condition factor were added to the model, neither of these variables explained boldness variation (for length: \( F_{1,139.72} = 0.922, P = 0.339 \), for condition: \( F_{1,160.76} = 0.641, P = 0.425 \)). There was no correlation between the difference between the first and the second boldness score and the number of days between the first and second behavioural test (Pearson’s \( R = -0.104, n = 67, P = 0.402 \)) indicating that the consistency of behaviour was independent of the measurement interval.

2.2 Predictors of vulnerability to fishing

Eighteen fish out of 117 were captured by angling in the fishing trials. Seventeen fish were captured only once, and one fish was captured three times. Logistic regression with stepwise term elimination indicated that condition factor after the fishing trials (Chanp of model, if term removed, \( P = 0.981 \)), residual boldness score (\( P = 0.444 \)) or condition factor prior to the fishing trials (\( P = 0.347 \)) had no impact on the probability to become captured by angling. However, fish length measured before the angling trials (\( B = 0.030, P = 0.001 \)) affected the capture probability positively. Also the population origin had a marginally significant effect (\( P = 0.087 \)), so that fish from Lake Kangasjärvi had higher probability to become captured than fish collected from the aquaculture ponds (\( p = 0.029 \)). The final model explained 32.5 % of the variance (Nagelkerke’s \( R^2 \)), and predicted 86.8 % of cases to correct vulnerability class.

When fish groups from each source of origin were analysed separately, the results changed marginally. None of the included variables explained vulnerability to angling for Lake Kangasjärvi fish (residual boldness score was the last eliminated term with \( P = 0.143 \)). Neither did any of the included variables explain vulnerability to angling among Lake Kivesjärvi fish (the fish length prior to the experiment was the last eliminated term with \( P = 0.185 \)). Among pond collected fish, longer fish (\( B = 0.090, p = 0.014 \)) had higher capture probability than smaller fish. Poor condition prior to the angling did not significantly increase capture probability (\( B = -32.77, P = 0.098 \)) but was included in the final model.

2.3 Angling-induced selection

Comparison of fish that become captured with fish that were not captured revealed that angling was selective for large body size among fish collected from the aquaculture ponds but not for other traits (Table 3, Fig. 2). Among all the fish, the residual boldness score did not differ between
captured (mean 0.022) and non-captured fish (mean -0.0026) (independent samples t-test, \( t = -0.229, df=114, P = 0.819 \)).

3 Discussion

Individually tested perch showed individually consistent behavioural differences in boldness independently of the time between the two trials indicating that perch clearly had CIDs in behaviour. The estimated repeatability of boldness (0.227) was relatively low but fell well with the commonly observed range of behavioural repeatabilities in fishes and other vertebrates (Bell et al., 2009). Significant repeatability also indicated that an estimate of the boldness could be achieved through a single test that was used for wild-collected fish. Kekäläinen et al., (2014) used similar individual tests and showed that individual boldness scores predicted behaviour also in groups in ecologically relevant conditions. This suggests that the experimentally obtained individual boldness scores in this study were ecologically meaningful (see also Rasmussen and Belk, 2012; Johnson et al. 2015) and indicated boldness-related behaviours such as exploration of novel arena containing predator cues and tendency to take risks. However, boldness did not predict vulnerability to angling statistically significantly within or across fish from different origins. Large body size was the most obvious predictor of vulnerability to angling.

Bold fish originating from domesticated hatchery strains of fish have been shown to be more susceptible to gill netting and angling than their less bold, wild specimens (Biro and Post, 2008; Klefoth et al., 2013). In contrast, our current results suggest that boldness does not explain vulnerability to angling in perch. These results, however, align with other studies that have not found a link between fish behaviour and vulnerability to fishing (Binder et al., 2012; Kekäläinen et al., 2014). Since the fish with differential background fishing history could not directly be compared due to the varying holding conditions and confounded population effect (Härkönen et al., 2015), the result of apparently higher angling vulnerability among wild-collected fish (by angling) in comparison to pond collected (by drying up the ponds) fish could not be confirmed. Anyhow, it was interesting that the wild-collected fish showing high vulnerability to angling (maybe because they had already been selectively captured by angling) were significantly less bold than the pond-collected fish in behavioural tests. This provides comparative evidence that high boldness does not explain high vulnerability to angling in perch and partially addresses the main weakness in our study: we were able to test the wild fish for boldness only once. Anyhow, it was interesting that the wild-collected fish showing high vulnerability to angling (maybe because they had already been selectively captured by angling) were significantly less bold than the pond-collected fish in behavioural tests. This provides comparative evidence that high boldness does not explain high vulnerability to angling in perch and partially addresses the main weakness in our study: we were able to test the wild fish for boldness only once. The wild-collected fish were larger than the pond-collected fish but the size difference was controlled statistically and could thus not explain all the population differences. The result of background influencing boldness supports previous studies in brown trout and perch (Härkönen et al., 2014, 2015).

The current results support earlier findings of angling being size-selective (e.g. Miranda and Dorr, 2000; Arlinghaus et al., 2008). However, the reasons for size-selectivity are not obvious (Stoner, 2004; Stoner and Ottmar, 2004; Vainikka et al., 2012). First, the hook size range that was used did not set any technical limitations why the smallest individuals could not have been captured. Second, direct measures of the satiation level of fish could not be obtained. It can be argued that in the experimental ponds, small fish had more food available that large individuals preferably feeding on small prey fish. This could have caused bias into the results on size-selectivity. Third, within-shoal dominance relationships may resolve which individuals will succeed in foraging in a social context, and consequently become captured in angling with natural bait (Koebele, 1985; Forrester, 1991; Alanärä and Brännäs, 1996; Tsuboi and Morita, 2004; Vainikka et al., 2012). As the most obvious factor explaining dominance in fishes is body size (Forrester, 1991), social dominance may have partially explained why the large fish were the most vulnerable to angling. However,
boldness was independent of fish length and as such opposed the prediction that large fish become captured easily because of their high boldness and thus dominant position (Vainikka et al., 2012).

Previous work has attempted to explain individual vulnerability to angling with multiple factors. Binder et al. (2012) found no support for the hypothesis that general activity or diel activity patterns would explain vulnerability to angling in the largemouth bass *Micropterus salmoides* groups selected for either high or low vulnerability to angling. However, the selected lines differed in metabolic rate so that high metabolic rate seemed to explain high vulnerability to angling (Redpath et al., 2010). Härkönen et al. (2014) found that highly explorative brown trout *Salmo trutta* were more vulnerable to fly fishing than less explorative trout. Wilson et al. (2011) showed that bold individuals of the bluegill sunfish *Lepomis macrochirus* were likely to become captured in open water by angling than the less bold conspecifics that were captured in refuge-like habitats, whereas in general angling targeted timid individuals. Wilson et al. (1993) found that seined pumpkinseed sunfish *Lepomis gibbosus* individuals differed in behaviour significantly from trapped individuals suggesting that individual behavioural differences may explain vulnerability to certain fishing methods, but also that the traits that make fish vulnerable to certain fishing method differ between fishing methods (see also Härkönen et al., 2015). Therefore, more studies on multiple species are needed before we can conclusively identify traits that expose fish to high fishing mortality.

Although certain traits may not directly explain vulnerability to angling, angling may still induce direct or correlated selection on them. Selectivity of fishing is in importance when assessing potential evolutionary consequences of it (Kuparinen et al., 2009). In the current study, angling was selective for size (Table 3). Previously, angling has been shown to be selective for a multitude of behavioural traits relating to foraging ecology (Nannini et al., 2011) and exploratory behaviour (Härkönen et al., 2014). Thus, the complex interactions involved in an angling situation deserve a lot more experimental research.

In conclusion, this study suggests that individual differences in boldness, as indicated by individual aquarium-scale tests under predator odour cues do not explain vulnerability to angling in Eurasian perch. Instead, large body size and wild origin predicted high vulnerability to experimental angling.

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References


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Table 1 Source of origin, number of fish, tagging date, mean size, mean condition factor, mean original boldness score (principal component score multiplied with -1, see 1.4 Data analysis) with standard deviations and capture success of the Eurasian perch used in the angling experiments

<table>
<thead>
<tr>
<th>Origin</th>
<th>n</th>
<th>Tagged</th>
<th>Length (mm)</th>
<th>Mass (g)</th>
<th>Condition</th>
<th>Boldness</th>
<th>Captured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kangasjärvi</td>
<td>33</td>
<td>29.6.2012</td>
<td>163.4 ± 19.1</td>
<td>45.9 ± 17.5</td>
<td>0.651 ± 0.044</td>
<td>-0.742 ± 0.683</td>
<td>14.5 %</td>
</tr>
<tr>
<td>Kivesjärvi</td>
<td>17</td>
<td>29.6.2012</td>
<td>182.4 ± 55.1</td>
<td>74.6 ± 61.3</td>
<td>0.606 ± 0.041</td>
<td>-1.131 ± 0.011</td>
<td>29.4 %</td>
</tr>
<tr>
<td>Ponds</td>
<td>67</td>
<td>18.9.2012</td>
<td>144.4 ± 42.3</td>
<td>43.7 ± 48.5</td>
<td>0.681 ± 0.043</td>
<td>0.326 ± 0.926</td>
<td>7.5 %</td>
</tr>
</tbody>
</table>

The tagging date refers to the date when the two-day tagging period was finished. Body size measures are taken straight after the angling experiments.

Table 2 Contribution of individual behavioural variables to boldness score (loadings in principal component analysis) and their repeatability (interclass correlation coefficients, ICC) in the Eurasian perch used in the angling experiments

<table>
<thead>
<tr>
<th>Variable</th>
<th>ICC</th>
<th>P</th>
<th>Loading</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to leave the start box</td>
<td>0.175</td>
<td>0.076</td>
<td>0.949</td>
</tr>
<tr>
<td>Time to reach the stones</td>
<td>0.106</td>
<td>0.193</td>
<td>0.961</td>
</tr>
<tr>
<td>Time to reach the open area</td>
<td>0.091</td>
<td>0.230</td>
<td>0.961</td>
</tr>
<tr>
<td>Time to reach the plants</td>
<td>0.071</td>
<td>0.282</td>
<td>0.952</td>
</tr>
<tr>
<td>Time to reach the wire-net</td>
<td>0.168</td>
<td>0.084</td>
<td>0.729</td>
</tr>
<tr>
<td>Time in the start box</td>
<td>0.063</td>
<td>0.304</td>
<td>N.A.</td>
</tr>
<tr>
<td>Time in the front of the start box</td>
<td>0.035</td>
<td>0.387</td>
<td>N.A.</td>
</tr>
<tr>
<td>Time in stony area</td>
<td>0.008</td>
<td>0.474</td>
<td>N.A.</td>
</tr>
<tr>
<td>Time in open area</td>
<td>0.078</td>
<td>0.263</td>
<td>N.A.</td>
</tr>
<tr>
<td>Time in vegetation</td>
<td>0.235</td>
<td>0.026</td>
<td>-0.791</td>
</tr>
<tr>
<td>Total number of zone crosses</td>
<td>0.340</td>
<td>0.002</td>
<td>-0.809</td>
</tr>
<tr>
<td>Freezing events</td>
<td>-0.051</td>
<td>0.662</td>
<td>N.A.</td>
</tr>
<tr>
<td>Total freezing time</td>
<td>0.090</td>
<td>0.232</td>
<td>-0.626</td>
</tr>
</tbody>
</table>

N.A. refers to “not available” as the original response variable was not included in the principal component analysis due to very poor and non-significant repeatability (ICC).
Table 3 Comparison of traits between *Perca fluviatilis* that were captured (n = 18) and were not captured (n = 99) in experimental angling

<table>
<thead>
<tr>
<th>Variable</th>
<th>Captured Mean</th>
<th>Captured S.E.</th>
<th>Not captured Mean</th>
<th>Not captured S.E.</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body length before angling</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Kangasjärvi</td>
<td>170.1</td>
<td>5.5</td>
<td>161.5</td>
<td>3.9</td>
<td>0.264</td>
</tr>
<tr>
<td>Lake Kivesjärvi</td>
<td>207.4</td>
<td>29.9</td>
<td>168.0</td>
<td>13.9</td>
<td>0.188</td>
</tr>
<tr>
<td>Pond fish</td>
<td>220.6</td>
<td>17.4</td>
<td>138.0</td>
<td>4.9</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Condition factor before angling</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Kangasjärvi</td>
<td>0.670</td>
<td>0.018</td>
<td>0.631</td>
<td>0.011</td>
<td>0.085</td>
</tr>
<tr>
<td>Lake Kivesjärvi</td>
<td>0.619</td>
<td>0.015</td>
<td>0.582</td>
<td>0.019</td>
<td>0.231</td>
</tr>
<tr>
<td>Pond fish</td>
<td>0.684</td>
<td>0.030</td>
<td>0.658</td>
<td>0.007</td>
<td>0.325</td>
</tr>
</tbody>
</table>

*P*-values are based on T-test of independent samples with appropriate correction for heteroscedasticity.
Fig. 1 Schematic figure of the experimental arena used to quantify individual behaviour in perch

Arena was floored with sand and gravel. The bottom of the plain area contained only fine sand.
None of the pairwise comparisons revealed statistically significant differences (independent samples t-test, $P \geq 0.252$). The numbers of captured fish were 8 for Lake Kangasjärvi, 5 for Lake Kivesjärvi and 5 for pond fish.