

Article

Does boldness explain vulnerability to angling in Eurasian perch *Perca fluviatilis*?

Anssi VAINIKKA^{a,*}, Ilkka TAMMELA^a, and Pekka HYVÄRINEN^b

^aDepartment of Biology, University of Eastern Finland, PO Box 111, FI 80101 Joensuu, Finland and ^bNatural Resource Institute Finland, Manamansalontie 90, 88300 Paltamo, Finland

*Address correspondence to Anssi Vainikka. E-mail: anssi.vainikka@uef.fi.

Received on 10 March 2015; accepted on 15 May 2015

Abstract

Consistent individual differences (CIDs) in behavior are of interest to both basic and applied research, because any selection acting on them could induce evolution of animal behavior. It has been suggested that CIDs in the behavior of fish might explain individual differences in vulnerability to fishing. If so, fishing could impose selection on fish behavior. In this study, we assessed boldness-indicating behaviors 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 behavior. Perch expressed repeatable individual differences in boldness-indicating behavior but the individual boldness-score (the first principal component) obtained using principal component analysis combining all the measured behavioral 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.

Key words: behavior, fishing-induced evolution, fishing vulnerability, growth, personality, selection.

Most animals including fishes display temporally consistent behavioral differences (CIDs) among individuals (Dall et al. 2004; Réale et al. 2007; Kortet et al. 2010; Stamps and Groothuis 2010). CIDs in behavior 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, that is traits that underlie observable behavioral 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 becomes which personality traits are the most important in affecting individual catchability (Wilson et al. 2011; Mittelbach et al. 2014).

CIDs in behavior 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 behavioral types (Wilson et al. 1993; Wilson et al. 2011; Härkönen et al. 2016). However, not all studies have found covariation between the CIDs in behavior 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 behavioral differences had a heritable basis, nonrandom mortality among behavioral types might induce evolution of animal personality or catchability through selection (Philipp et al. 2009). Because 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 behavior are potentially severe and therefore require attention (Uusi-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 behavioral ecology (e.g. Westerberg et al. 2004; Heibo and Magnhagen 2005; Heibo et al. 2005). Perch show individually consistent behavioral 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).

Materials and Methods

Fish

To increase variance among fish and thus our potential to find general links among behavior, 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 accidentally 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 naïve 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 that is more 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 aminobenzocaine “benzocaine” 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.

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 (Figure 1) between 19th of September 2012 and 21st of October 2012 (Figure 1). The arena contained a start tube, two shelter areas (with stones or plastic plants), and an open space between the shelter areas. The behavioral 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

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 “Data analysis” section) with standard deviations and capture success of the Eurasian perch used in the angling experiments

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

The tagging date refers to the date when the 2-day tagging period was finished. Body size measures are taken straight after the angling experiments.

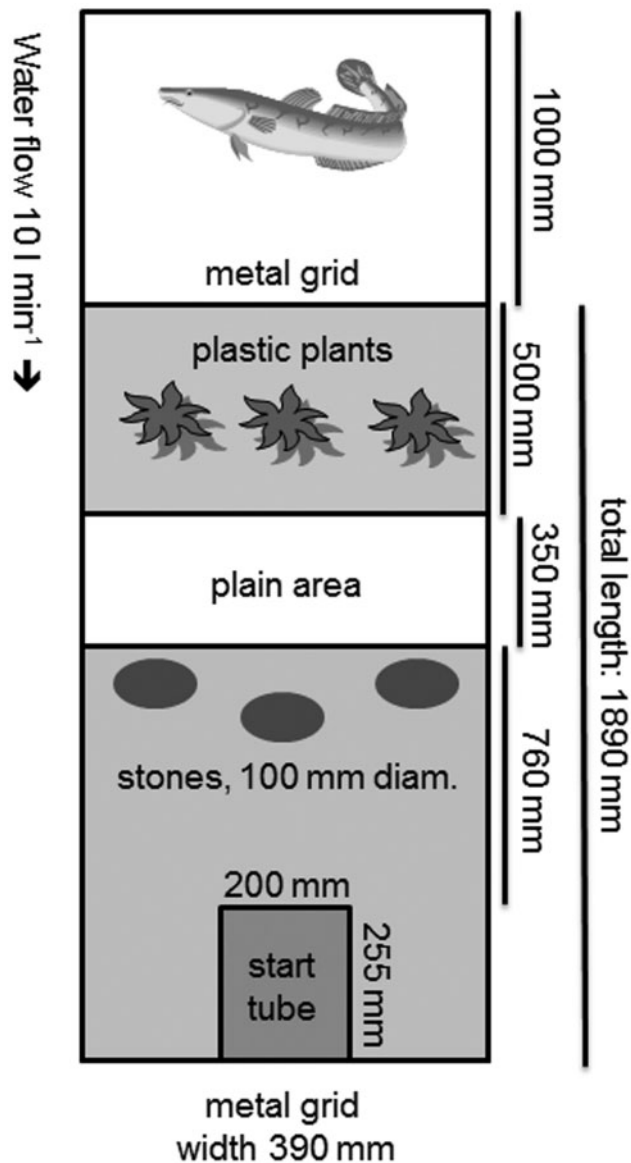


Figure 1. Schematic figure of the experimental arena used to quantify individual behavior in perch. Arena was floored with sand and gravel. The bottom of the plain area contained only fine sand.

the experiments and varied between 5.6°C and 11.9°C. Water oxygen concentration varied between 9.4 mg l⁻¹ and 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 behavior 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 min before the door was remotely opened and fish behaviors 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 behavioral experiments, fish were anesthetized (see above), measured for length and body mass, and returned to a 3.2-m² fiberglass holding tank to wait for the second trial or transferred to the outdoor angling ponds (see below). All the behavioral experiments were performed by a single person (I.T.).

Fishing trials

Directly after the last behavioral test on 11th–21st of October 2012, the fish were randomly divided into two similar, rectangular 400 m² 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 30th of October 2012 and 3rd of November 2012. Water temperature during the angling trials was 3–5°C. Final effort of 1 h per pond was invested in the morning of 4th 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-colored 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 losing 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 color 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, $K = 100 \text{ g}^{-1} \cdot \text{cm}^b$ total body mass (g) (total body length (cm))^{-b}, where b (3.15355) was obtained as the slope of a regression of $\ln(\text{weight})$ on $\ln(\text{total length})$ using all the data pooled from the measurements (linear regression, $R^2 = 0.941$, $n = 232$, $P < 0.001$, Bolger and Connolly 1989).

Data analysis

Ln-transformed (in order to meet normality) behavioral 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 behavioral test (as day number from 1st January 2012), time of behavioral 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 behavioral 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 behavior would

Table 2. Contribution of individual behavioral 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

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

NA refers to "not available" as the original response variable was not included in the principal component analysis due to very poor and nonsignificant repeatability (ICC).

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 nonsignificant 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 noncaptured fish within and across different origins. Experimental ponds were assumed similar and their potential effects were not modeled 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).

Results

Behavioral 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 min for all the fish. On average, the fish spent 3.3 min among the plastic plants close to the predator section. Freezing behavior was common; the average freezing time was 5.2 min.

Principal component analysis revealed that all the determined behavioral variables could be described effectively by a single principal component (Table 2) that accounted for 73.2% of the total variance in behavior (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% CI -0.001 to 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 behavioral 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 behavioral test within a day ($F_{1,153.41} = 0.081$, $P = 0.776$) did not significantly explain behavioral 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 behavioral 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 behavioral test (Pearson's $R = -0.104$, $n = 67$, $P = 0.402$) indicating that the consistency of behavior was independent of the measurement interval.

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 (Change 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 analyzed 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.

Angling-induced selection

Comparison of fish that became 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, Figure 2). Among all the fish, the residual boldness score did not differ between captured (mean 0.022) and noncaptured fish (mean -0.0026) (independent samples t -test, $t = -0.229$, $df = 114$, $P = 0.819$).

Table 3. Comparison of traits between *Perca fluviatilis* that were captured ($n = 18$) and were not captured ($n = 99$) in experimental angling

Variable	Captured		Not captured		Sig.
	Mean	SE	Mean	SE	
Body length before angling					
Lake Kangasjärvi	170.1	5.5	161.5	3.9	0.264
Lake Kivesjärvi	207.4	29.9	168.0	13.9	0.188
Pond fish	220.6	17.4	138.0	4.9	<0.001
Condition factor before angling					
Lake Kangasjärvi	0.670	0.018	0.631	0.011	0.085
Lake Kivesjärvi	0.619	0.015	0.582	0.019	0.231
Pond fish	0.684	0.030	0.658	0.007	0.325

P values are based on t -test of independent samples with appropriate correction for heteroscedasticity.

Discussion

Individually tested perch showed individually consistent behavioral differences in boldness independently of the time between the two trials indicating that perch clearly had CIDs in behavior. The estimated repeatability of boldness (0.227) was relatively low but fell well with the commonly observed range of behavioral 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 behavior 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 behaviors 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 behavior and vulnerability to fishing (Binder et al. 2012; Kekäläinen et al. 2014). Because 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. 2016), 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 behavioral 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

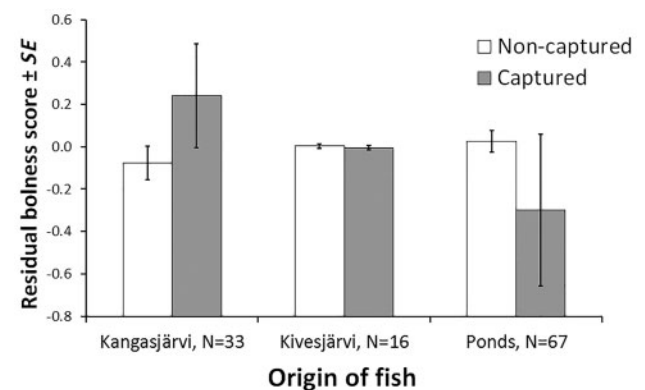


Figure 2. Comparison of residual boldness score between captured and non-captured perch among different origins of fish. None of the pairwise comparisons revealed statistically significant differences (independent samples t -test, $P \geq 0.252$). The numbers of captured fish were 8 for Lake Kangasjärvi, 5 for Lake Kivesjärvi, and 5 for pond fish.

all the population differences. The result of background influencing boldness supports previous studies in brown trout and perch (Härkönen et al. 2014, 2016).

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 than 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 behavior significantly from trapped individuals suggesting that individual behavioral 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. 2016). 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 behavioral traits relating to foraging ecology (Nannini et al. 2011) and exploratory behavior (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 odor cues do not explain vulnerability to angling in Eurasian perch. Instead, large body size and wild origin predicted high vulnerability to experimental angling.

Funding

This research has been supported by a grant from the Emil Aaltonen foundation.

Acknowledgments

Staff of the Kainuu fisheries research station of Finnish Game and Fisheries Research Institute is acknowledged for their help in the practical arrangements of the experiments. All the animal experimentation was performed under a license ESAVI/4356/04.10.03/2011.

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