

# Behavioural variation in Eurasian perch populations with respect to relative catchability

Laura Härkönen<sup>1,3</sup> · Pekka Hyvärinen<sup>2</sup> · Petri T. Niemelä<sup>1,3</sup> · Anssi Vainikka<sup>1,3</sup>

Received: 20 November 2013 / Revised: 30 January 2015 / Accepted: 26 April 2015 / Published online: 8 May 2015  
© Springer-Verlag Berlin Heidelberg and ISPA 2015

**Abstract** Animal personalities, i.e. consistent individual differences in behaviour, are currently of high interest among behavioural and evolutionary biologists. The topic has received increasing attention also in fisheries science because selective harvesting of certain behavioural types might impose fishing-induced selection on personality. Here, we ice-fished wild Eurasian perch (*Perca fluviatilis*) from three native populations and investigated whether differences in relative catchability would explain behavioural differences observed in experimental conditions. We inferred relative catchability differences indirectly by fishing each location first with generally inefficient artificial bait and then by more efficient natural bait. The captured, individually tagged fish were tested in groups for their exploration tendency, activity and boldness under authentic predation risk in semi-natural stream channels. Fish that were easily captured first with artificial bait expressed fast exploration and acute activity, whereas the fish captured with natural bait showed less active and explorative behaviour. Differences in relative catchability did not explain variation in boldness or body size. In conclusion, we found that (1) Eurasian perch differing in relative catchability differ in certain behavioural traits, (2) fast explorers are more common among fish that get easily caught compared to fish that

are more difficult to catch, (3) relative catchability explains more behavioural variation in a novel environment than in a familiar one and (4) selectivity of recreational angling on fish behaviour may depend on applied angling method and the effort spent on each location.

**Keywords** Angling · Animal personality · Capture method · Exploration · Fisheries-induced selection · Group behaviour

## Introduction

Animal personalities, i.e. consistent behavioural differences among individuals across time and different contexts, have been of high interest among behavioural ecologists during the last decade (Sih et al. 2004; Réale et al. 2010; Stamps and Groothuis 2010; Mittelbach et al. 2014). Recently, they have also received increasing attention in applied contexts, such as among studies on harvesting-induced evolutionary changes (Wilson et al. 2011; Binder et al. 2012; Härkönen et al. 2014). In particular, selective harvesting of certain behavioural types has been predicted to impose fishing-induced selection on fish personality (Lewin et al. 2006; Uusi-Heikkilä et al. 2008; Conrad et al. 2011). According to current knowledge, individual fish differ in their vulnerability to angling (Tsuboi and Morita 2004), and recreational fishing can induce evolution of vulnerability to fishing, i.e. catchability (Philipp et al. 2009). Recent experimental evidence shows that phenotypic changes induced by size-selective harvesting may have a genetic basis (van Wijk et al. 2013) underlining the importance of examining the consequences of fishing-induced selection. By now, there is very little knowledge of how individuals captured with different methods might differ behaviourally (Wilson et al. 2011) while the question is crucial

✉ Laura Härkönen  
laura.harkonen@oulu.fi

<sup>1</sup> Department of Biology, University of Eastern Finland, P.O. Box 111, FI-80101 Joensuu, Finland

<sup>2</sup> Natural Resources Institute Finland (Luke), Natural Resources and Bioproduction, Manamansalontie 90, FI-88300 Paltamo, Finland

<sup>3</sup> Department of Biology, University of Oulu, P.O. Box 3000, FI-90014 Oulu, Finland

when estimating the total selection induced by multi-gear fishery.

Catchability is defined as the efficiency of a particular fishery to remove individuals from a population in relation to used fishing effort (Arreguín-Sánchez 1996). The role of fish behaviour contributing to catchability is of highly topical interest considering the recent evidence for the existence of heritable personality traits in fish (van Oers and Sinn 2013; Kortet et al. 2014). Animal personalities describe, for example, consistent individual differences in general activity, tendency to explore or avoid novelty, willingness to accept risks (such as whether to feed in the presence of predators) or aggression towards conspecifics (Dall et al. 2004; Réale et al. 2007; Stamps and Groothuis 2010). Bold and aggressive behaviours, in particular, are predicted to play an important role in vulnerability to angling because they often contribute to high foraging rate (Uusi-Heikkilä et al. 2008; Biro and Post 2008). Addressing the importance of behavioural traits in explaining vulnerability to fishing would be valuable in natural conditions in particular. However, in the wild, it is rarely possible to make observations on fish that do not become captured, and one must rely on observable differences in relative catchability. Relative differences in catchability can be estimated by capture order so that more vulnerable fish are likely to be captured earlier than less catchable fish (Vainikka et al. 2012a) and potentially by using angling gear that differ in their attractiveness to the fish.

Eurasian perch (*Perca fluviatilis* L.) is the most popular target species of recreational fishers in Finland (Anonymous 2011). The perch are known to express consistent behavioural differences among individuals that are impacted but not overwhelmed by social effects (Magnhagen and Bunnefeld 2009). In addition, different perch populations are known to differ in their behaviour (e.g. in their risk-taking tendency; Magnhagen et al. 2012). While Kekäläinen et al. (2014) did not find clear evidence that Eurasian perch captured with different angling methods in a dense population would differ in experimentally observed behaviour, it is yet unknown whether the predicted link between behavioural variation and catchability would be present in certain populations and when amplified by combining the capture order effect with angling gear effect.

Our principal aim was to test if relative catchability of Eurasian perch would explain behavioural variation in laboratory conditions. We angled wild perch from three native populations and applied two different angling methods that were assumed to differ in their efficiency to catch wild perch. Based on our long experience in ice fishing, we made the a priori prediction that a fully artificial lure—a novel object that resembles an unnatural prey item—is less efficient in catching perch than natural bait, i.e. a Chironomid larva representing a typical natural food item for perch. This assumption was based on the authors' personal observation that anglers catch

more fish with natural bait in any given location, even when no fish would attack the artificial bait (an assumption also confirmed in this study). In other words, we predicted that if certain behavioural traits, such as high explorativeness, activity or boldness, increase the catchability, these two methods used consecutively should yield perch with distinguishable behavioural types. At each fishing location, we first used the *artificial method* and expected to capture the boldest (and most active and explorative) fish, whereas the shyer individuals from the same location were expected to be captured later with the more efficient *natural method*, i.e. we expected boldness to decrease with decreasing relative catchability. In order to assess behavioural variation with respect to relative catchability, we used long-term automatic monitoring of individual behaviour in replicated groups in semi-natural environments.

## Materials and methods

Ice fishing—angling through a hole in the ice—is a common activity, especially in Fennoscandia and northern parts of North America (Nuttall et al. 2004). Experienced ice fishers (A. Vainikka and P.T. Niemelä) sampled the fish from three native Eurasian perch populations in Central Finland in late winter 2012. In the mesotrophic Lake Oulujärvi (27° 10' E, 64° 20' N, mean depth 7.6 m, surface area 928 km<sup>2</sup>) there were two distinct sampling sites, Mieslahti Bay and Martinlahti Bay, located ca. 39 km apart from each other. Mieslahti Bay is eutrophic and has clearly humic water. More oligotrophic Martinlahti Bay is located in the middle of Lake Oulujärvi and has clearly less humic water than Mieslahti Bay. We use the term population here bearing in mind the likely gene flow but different environmental characteristics between the sites. The third sampling site, Lake Kivesjärvi (27° 26' E, 64° 26' N, mean depth 4.0 m, surface area 27 km<sup>2</sup>), is clearly humic, nearly eutrophic and discharges to Lake Oulujärvi.

## Sampling order and methods

The sampling procedure followed a typical ice fishing routine: the fish were actively sought by drilling holes (115 mm in diameter), and if no fish were caught from a hole, a new hole was drilled ca. 50–200 m apart from the old one. Once an area with perch was found, the distance between the holes was at least 5 m. Perch were always fished 5–20 cm from the bottom of the lake, as small perch individuals very rarely enter the free water column (personal observation).

At each new fishing hole, the angling started with a fully artificial lure (ViM 34 mm, ViM Pirken, Sweden, along with #14 coloured (#013) Mustad 73028 triple hook) and continued until no fish attacked the lure for a minute (60 s). The angling

continued with natural bait (2–4 live Chironomidae, i.e. bloodworms) using an inconspicuous, small copper-coloured Mormyshka with a single #14 hook. Fishing continued until no fish attacked the bait for a minute. Thereby, each trial took at least 2 min (i.e. 1 min/method/hole if no fish were caught). These lure types are not typical only for ice fishing, since different artificial lures as well as natural baits are commonly used in several recreational angling methods (Arlinghaus et al. 2008).

For simplicity, the two catch groups differing in relative catchability, i.e. (1) perch captured first with artificial lures and (2) perch captured later with natural baits, will be referred to according to the angling gear as artificial method and natural method. It should be noted that the reference to angling method includes also the capture order effects (on purpose): the lure type was changed along the capture order with the intention to amplify the assumed selectivity on different behavioural types.

Altogether, 67 perch were captured from Mieslahti Bay (28 March 2012), 30 perch from Martinlahti Bay (27 March 2012) and 78 perch from Lake Kivesjärvi (between 26 March and 2 April 2012). Excluding the holes where no perch were caught, 19, 18 and 25 holes were sampled in the three populations, respectively.

## Handling of the fish

Once captured, the fish were carefully released from the hook and placed in a 10-l bucket filled with 5 l of water and standard solution of benzocaine (40 mg/l) for anaesthetization. During anaesthesia, a 12.0×2.12 mm PIT-tag (HDX ISO 11784/11785 compliant ICAR-registered animal tag, read-only, weight 0.1 g; OregonRFID Inc., [www.oregonrfid.biz](http://www.oregonrfid.biz)) was placed under the skin next to the dorsal fin. After tagging, the fish were transported to the Kainuu Fisheries Research Station (64° 23' 20" N, 27° 30' 23" E). There, the fish were held in 3.4 m<sup>2</sup> tanks supplied with water of ambient temperature (<4 °C) from nearby Lake Kivesjärvi. The light rhythm followed the natural light rhythm in the study area. The fish were provided with fish food pellets twice a week.

On 2 April 2012, the fish were measured for total length and body mass during anaesthesia induced by benzocaine (40 mg/l). Adjusted body condition index,  $K$  was calculated using the equation,

$$K = 100 \text{ g}^{-1} \text{ cm}^b \times \text{total body mass (g)} \\ \times \text{total body length (cm)}^{-b} \quad (1)$$

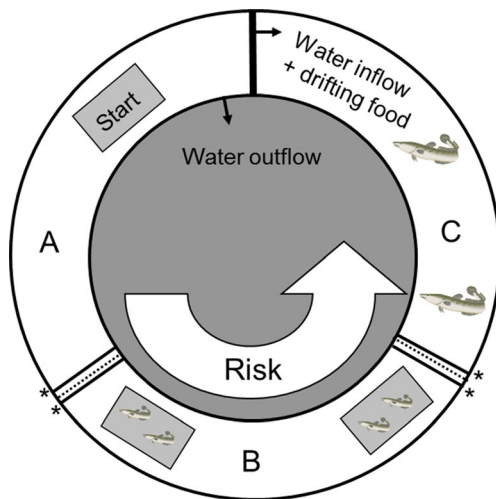
where  $b$  (3.326) was obtained as the slope of a regression of  $\ln(\text{body mass})$  on  $\ln(\text{total length})$  of all perch (Bolger and Connolly 1989).

## Behavioural experiment

In order to test whether the perch captured with artificial and natural methods exhibit different behaviour, we conducted a 13-day experiment in semi-natural environment in April 2012 (see also Kekäläinen et al. 2014). Individual behaviour was followed in groups, since perch is a strong schooling species and probably becomes stressed in isolation (Magnhagen and Bunnefeld 2009). Five replicate groups were tested for behaviour in circular, gravel-bottomed, concrete outdoor channels (outer circumference 30.9 m, inner circumference 26.0 m, one circle 28.45 m, channel width 1.5 m, water depth on average 333 mm). The experimental streams were covered with dark green plastic tents and supplied with lake water from Lake Kivesjärvi (directional water flow of 0.11 m·s<sup>-1</sup>/55 l·s<sup>-1</sup>).

The burbot (*Lota lota*), used as an authentic predator cue in this study, is a nocturnal predator to which perch react by behavioural antipredatory responses but which, in comparison to pike (*Esox lucius*), rarely manage to forage on prey fish in experimental conditions (Ylönen et al. 2007). To first confirm the intimidation effect of burbot, a preliminary experiment was conducted in July–August 2011 in the same streams (8 channels, 128 perch). Each stream was divided into two replicates: eight replicate streams had two burbot in a grid-separated half and the remaining eight streams were used as predator-free controls (similar experimental design explained in detail in Rodewald 2013). When burbot were present in the streams, the perch avoided the burbot section, and the intimidation effect was statistically significant (RM-ANCOVA:  $F_{1, 49}=6.30$ ,  $P=0.015$ ; Merihaara U-M, unpublished data). Thus, no control streams were used in this study (nor were they available).

For this study, the stream channels were divided into three sections (A: safe, B: potential risk, C: real risk, Fig. 1). Prior to the experiment, the fish were allowed to acclimatise to the streams for one day. For acclimatisation, the perch were placed in boxes (in 400×560×755 mm boxes with open 10×10 mm wire net ends) in the predator-free downstream section A. Two similar boxes, both inhabited by two small burbot (100–300 g, 25–35 cm), were placed in section B creating a potential predation risk for the perch: during the experiment, these burbot were kept in the boxes, but they were visually detectable by the perch. In section C with real predation threat, two large burbot (800–1200 g, 45–60 cm) were roaming freely. The movement of burbot in the streams was limited within the section C by wire nets (pentagonal mesh: width 28 mm, height 37 mm) placed between the sections B and C, which excluded the use of the largest perch that could not pass the nets (16.7 % of all captured perch). Thus, a total of 145 perch smaller than 188 mm/62 g ( $N=80$  with artificial lure;  $N=65$  with natural bait) were randomly (but equally with respect to population; 57 perch from Lake Kivesjärvi, 29 from Martinlahti Bay and 59 from Mieslahti Bay) distributed into the streams ( $N=29$  fish per stream).



**Fig. 1** The experimental setup for the observation of behaviour in groups in a semi-natural environment. Asterisks indicate the places of four PIT antennas; one antenna was placed on both sides of the net gates dividing the experimental streams into three sections. In the figure, *A* represents the safe section, *B* potential risk with predators in boxes and *C* authentic risk with free predators

No additional food was provided to the fish during the experiment, but the gravel bottom in the entire stream channel supports natural benthic prey. The density of drifting food items, e.g. crustacean mysids (*Mysidae*; Rodewald et al. 2011) was assumedly highest in the predator zone where the water inlet was situated (Fig. 1). No mortality was detected between the capture and the end of the behavioural experiment. After day 13, the fish were returned into indoor tanks for further experiments (not described here).

### Behavioural measurements

The data on individual behaviour within replicated groups were collected automatically. The wire net gates between the sections A-B and B-C were equipped with two PIT antennas, one at both sides of each gate. The antennas were connected to computers that recorded signal detections nine times in a second ( $9\text{ s}^{-1}$ ; see Vainikka et al. 2012b for details). The individual position in each of the zones was calculated at 1-min precision using the PIT Data: Software for analyzing data from PIT tags (<http://www.pitdata.net>). The 1-min resolution data were further analysed using custom codes in AV Bio-Statistics software (developed by A. Vainikka) to calculate (1) *exploration* as the time taken before entering the predator section C for the first time, (2) *general activity* as total number of antenna bypasses per day and (3) *space use* as minutes per day that an individual spent in the predator section, the section with potential risk and the safe section (boldness).

A boldness-indicating score for each individual was assessed by performing a principal component analyses (PCA) in which the data on space use in relation to the degree

of predation risk (i.e. 13 daily repeated measures for each individual) were used. In the PCA, the minutes per day that an individual spent in safe, risky and predator sections were used as continuous, ln-transformed variables. The only principal component (PC1) given by the procedure explained 54 % of the variation in space use (Table 1). PC1 was considered as a good estimate of boldness under predation risk by giving low scores for shy individuals avoiding predator section(s) and staying mostly in the safe area, and high scores for bold individuals that stayed also in the sections with potential or real predation risk.

Preliminary examination of the data on individual movements in experimental stream revealed a strong effect of the habituation on general activity and boldness scores (PC1). The temporal variation in individual movements stabilised markedly after the first 3 days, which was taken as an indication that habituation to experimental streams had occurred (see Fig. 2). Thus, the 13-day observations were divided into acute (days 1–3) and long-term (days 4–13) periods for further examination. Acute behaviour in novel environment was assessed as (1) *exploration*, and as repeated measurements data on (2) *acute activity* and (3) *acute boldness* (PC1). The long-term behaviour was quantified as repeated measures of behaviour after habituation as (4) *long-term activity* and (5) *long-term boldness* (PC1).

### Statistical analyses

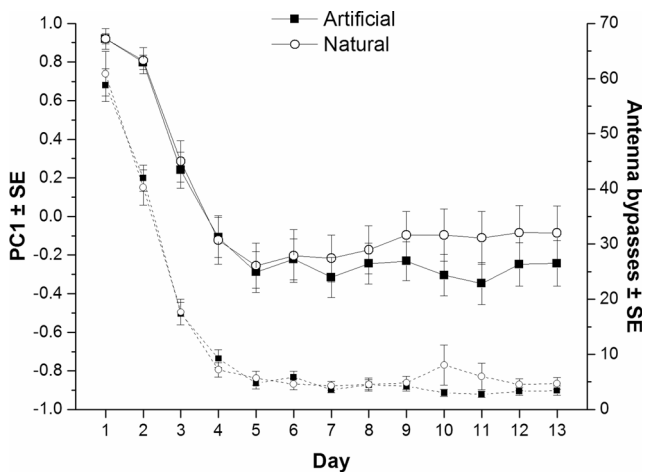
In order to analyse whether different measures of individual behaviour (1–5; see above) or size-related traits (body length, weight or body condition index) differ between the angling methods (relative catchability groups) and populations, we used general(ised) linear mixed effect modelling. The statistical analyses were performed in SPSS 21.0 for Windows (IBM, USA).

The data on exploration was significantly skewed towards large values, and thus, a generalised linear mixed effects model with gamma distribution and log link function was fitted for

**Table 1** Results from principal component analysis (PCA) based on three elements describing the space use in relation to predation risk in a semi-natural environment

	PC1
Time in section A (safe)	−0.767
Time in section B (potential risk)	0.869
Time in section C (authentic risk)	0.523
Eigenvalue	1.619
Percentage of variance explained	53.96

Trait loadings, eigenvalue and explained variance are given to the component. Sample size is 145 individuals each measured 13 times (i.e. days)



**Fig. 2** Long-term development of activity and boldness scores with respect to angling method. Boldness (PC1±SE) is represented by *large plots* and *solid lines* while activity (total antenna bypasses±SE per day) is shown as *small plots* and *dashed lines*

the data. The full model included angling method and population as explanatory variables. Fishing location (i.e. hole nested within the population) and individual subject as well as the replicate groups (i.e. stream) were included as random effects in the model. The size variable (length, weight or body condition index), having the highest explanatory power for behavioural variation, was included in the model. Interaction terms were reduced in parsimony until the best model goodness-of-fit was obtained according to the Akaike’s information criteria (AIC) and by visual evaluation of residual plots.

The variation in activity (total number of daily antenna bypasses was ln-transformed to obtain normality) and boldness scores (PC1) with respect to angling method and population was analysed separately for overall, acute and long-term variation using general linear mixed effect model with repeated measures. The models for overall variation in both variables included repeated measures of moving activity and boldness scores throughout the experiment. The models for acute variation either in activity or boldness included repeated behavioural measures for the first 3 days, whereas the models for long-term variation included the measures for the 10 following days. Each of the full models included the population and angling method (relative catchability group) as fixed factors, and random effect of fishing location (i.e. the hole nested within population), individual and replicate group. The size variable with the greatest effect on behavioural variation was included in the model as fixed effect. The non-significant fixed effects, covariates and interactions were removed according to the principle of parsimony and the final model was chosen according to the lowest AIC value.

The among-individual consistency of perch activity and boldness was evaluated by calculating repeatability (*r*), i.e.

the proportion of variation in both traits that is due to differences among individuals. The significance of among-individual variation was defined by comparing 2\*Δlog-likelihood of full model and the model where the focal random effect of interest (individual) was restricted to zero using  $\chi^2$  test over 1 degree of freedom (likelihood ratio test, LRT; see Dingemanse and Dochtermann 2013 and references therein). While the models in comparison either included or excluded individual as a random effect, they simultaneously controlled the variance components for the fixed and random factors (assessed as in the generalised linear mixed models (GLMMs) for activity and boldness above). Because the exploration could be measured only once for each individual, the repeatability could not be assessed.

Differences in size-related traits (body length, weight and body condition index) with respect to angling method and population were analysed using general linear mixed effect models. In the full models, fixed effects of population and angling method as well as their interaction term were first included. Interaction term was removed if it was statistically non-significant ( $P>0.05$ ). The fishing location within a population was entered in the model as a random effect. Analyses on all size-related traits included all the captured fish, i.e. also those that were excluded from the behavioural experiment.

## Results

### Consistency of between-individual variation in activity and boldness during the experiment

The variance in general moving activity showed significant repeatability among individuals throughout the experiment ( $r=0.16$ , LRT:  $\chi^2=521.924$ ,  $df=1$ ,  $P<0.001$ ), while the variance explained by the replicate group was low (2 %). Once introduced to the streams, all perch were highly active and switched between different sections up to 142 times during the first day (mean±SE 59.74±2.41). During the first 3 days, activity rapidly decreased, after which the activity was stabilised at a relatively low level as the fish moved between the sections less than five times a day on average (mean±SE 4.64±0.23; Fig. 2). Due to substantial habituation effect and individually similar rate of habituation, the highest variance (82 %) occurred within the individuals during the first 3 days. The overall activity was significantly affected only by body condition (Table 2): perch in good condition were more active throughout the study ( $B\pm SE=6.683\pm 3.049$ ).

The between-individual differences in boldness-indicating PC1 score also showed significant repeatability ( $r=0.44$ , LRT:  $\chi^2=1068.578$ ,  $df=1$ ,  $P<0.001$ ). However, 54 % of variation was due to within-individual differences as all perch scored significantly higher for their acute boldness than after

**Table 2** Statistics of general(ised) linear mixed effects models for the behavioural measures within different time frames

Time frame	Source of variation	<i>df</i>	<i>df</i> denom.	<i>F</i>	Sig.	
Throughout the experiment	(1) Overall activity					
	Intercept	1	139.481	0.991	0.321	
	Angling method	1	139.481	0.141	0.708	
	Population	2	139.481	0.010	0.990	
	Body condition	1	139.481	4.805	0.030	
	(2) Overall boldness (PC1)					
	Intercept	1	136.979	3.221	0.075	
	Angling method	1	136.979	0.303	0.583	
	Population	2	136.979	3.157	0.046	
	Body condition	1	136.979	2.858	0.093	
	Population × body condition	2	136.979	3.165	0.045	
	Novel environment	(3) Exploration				
		Corrected model	7	136	2.918	0.007
		Angling method	1	136	3.618	0.002
		Population	2	136	3.360	0.029
		Weight	1	136	1.347	0.248
Angling method × population		2	136	0.071	0.931	
Angling method × weight		1	136	11.147	0.001	
(4) Acute activity						
Intercept		1	139.544	1.286	0.259	
Intercept		1	126.432	991.811	<0.001	
Angling method		1	126.432	4.017	0.047	
Population		2	126.432	3.370	0.038	
Weight		1	126.432	6.126	0.015	
Angling method × weight		1	126.432	5.893	0.017	
Angling method × population		2	126.432	2.771	0.066	
(5) Acute boldness (PC1)						
Intercept	1	132.275	231.478	<0.001		
Angling method	1	132.275	0.316	0.575		
Population	2	132.275	3.482	0.034		
Weight	1	132.275	5.992	0.016		
Population × weight	2	132.275	5.075	0.008		
Familiar environment	(6) Long-term basal activity					
	Intercept	1	139.544	1.286	0.259	
	Angling method	1	139.544	0.181	0.671	
	Population	2	139.544	0.006	0.994	
	Body condition	1	139.544	0.998	0.027	
	(7) Long-term boldness (PC1)					
	Intercept	1	137.415	3.107	0.080	
	Angling method	1	137.415	0.344	0.558	
	Population	2	137.415	3.218	0.043	
	Body condition	1	137.415	2.663	0.105	
	Population × body condition	2	137.415	3.221	0.043	

habituation. While exploring the environment during the first 3 days of the study, all the fish visited every section: the boldest perch entering the final section (C) only after 4 min while it took for 34 h for the shyest individual to enter the section. In the long term, the low-explorative fish were also

more likely to avoid the risky sections later as indicated by the significant repeatability of behavioural pattern of individuals over the entire study period. The variance explained by random group effects was low (2 %). The overall boldness differed significantly between populations, as the perch from

Martinlahti Bay were the boldest and the perch from Kivesjärvi the shyest (Tables 2 and 3). Boldness was significantly affected also by population×body condition interaction: perch in good condition were bold in Lake Kivesjärvi and Martinlahti Bay, while those in low body condition were bold in Mieslahti Bay.

**Behaviour in novel environment**

Perch captured with the artificial lure, i.e. with high relative catchability, showed greater exploration and acute activity: they entered the section with real risk of predation earlier (Fig. 3a) as well as showed a higher number of antenna bypasses during the first 3 days of the experiment (Fig. 3b), than the individuals with lower relative catchability, i.e. those captured with natural bait (Table 2). Acute boldness did not differ between these groups (Fig. 3c).

All the variables measuring behaviour in a novel environment differed significantly between the populations (Table 2). The fish captured from Martinlahti Bay were more explorative and exhibited higher acute activity and greater acute boldness (PC1 scores) than the fish captured from Lake Kivesjärvi or Mieslahti Bay (Table 3). There were no significant populations by method interactions in any of the variables describing behaviour in novel environment.

During the modelling process, body weight was found to be the most important size-related predictor for the behaviour in novel environment (Table 3). The small individuals had significantly higher acute activity ( $B \pm SE = -0.03 \pm 0.006$ ) and boldness scores ( $B \pm SE = -0.004 \pm 0.004$ ) compared to large individuals. In addition, as indicated by significant body weight by angling method interactions (Table 2), the large

individuals exhibiting low acute activity and acute boldness scores were more often captured with natural baits. Body weight had no significant main effect on exploration, but the body weight interacted with population (Table 2): among the perch angled from Mieslahti Bay, the body weight did not affect exploration, while among the perch from Lake Kivesjärvi, in particular, the largest individuals exhibited the slowest exploration.

**Behaviour after habituation**

Once the perch habituated to environmental streams, either long-term activity (Fig. 3d) or boldness (Fig. 3e) did not differ between the angling methods (Table 2). Body condition was the most important size-related predictor for both of the long-term behavioural measures. Long-term activity was significantly affected only by body condition (Table 2); increased activity was observed among perch with high body condition ( $B \pm SE = 6.942 \pm 3.105$ ). Long-term boldness, instead, was affected by population and its interaction with body condition (Table 2). The perch from Martinlahti Bay exhibited the highest long-term boldness scores, whereas the perch from Lake Kivesjärvi had the lowest scores (Table 3). In both Martinlahti Bay and Lake Kivesjärvi, low body condition was associated with low boldness scores, whereas in Mieslahti Bay, the perch in low body condition exhibited higher boldness scores than those in good condition.

**Perch size and condition**

Perch captured with different methods did not differ in their body weight ( $F_{1, 131.526} = 2.653, P = 0.106, \text{Fig. 3f}$ ), body

**Table 3** Population differences in terms of estimated means of behavioural and life history traits in different contexts

Context	Measured trait	Population		
		Lake Kivesjärvi	Martinlahti Bay	Mieslahti Bay
Through the study	Overall activity <sup>b,c</sup>	1.042±0.111 (1.835)	1.067±0.153 (1.907)	1.056±0.107 (1.875)
	Overall boldness (PC1±SE)	-0.221±0.111	-0.058±0.154	-0.132±0.107
Behaviour in novelty	Exploration <sup>a</sup> (min±SE)	81.650±25.477	34.733±12.498	88.832±27.451
	Acute activity <sup>b,c</sup>	3.655±0.085 (37.67)	4.017±113 (54.53)	3.755±0.081 (41.723)
	Acute boldness (PC1±SE)	0.857±0.041	0.952±0.056	0.879±0.040
Long-term behaviour	Activity <sup>b,c</sup>	0.980±0.113 (1.664)	1.000±0.156 (1.718)	0.984±0.109 (1.675)
	Boldness (PC1±SE)	-0.262±0.116	-0.107±0.161	-0.176±0.112
Sampling	Body length (mm) <sup>c</sup>	5.027±0.054 (151.47)	4.975±0.058 (143.75)	4.928±0.054 (137.10)
	Body weight (g) <sup>c</sup>	3.399±0.186 (28.93)	3.205±0.201 (23.66)	3.062±0.188 (20.37)
	Body condition index (K) <sup>c</sup>	0.293±0.002 (0.340)	0.290±0.002 (0.335)	0.289±0.004 (0.336)

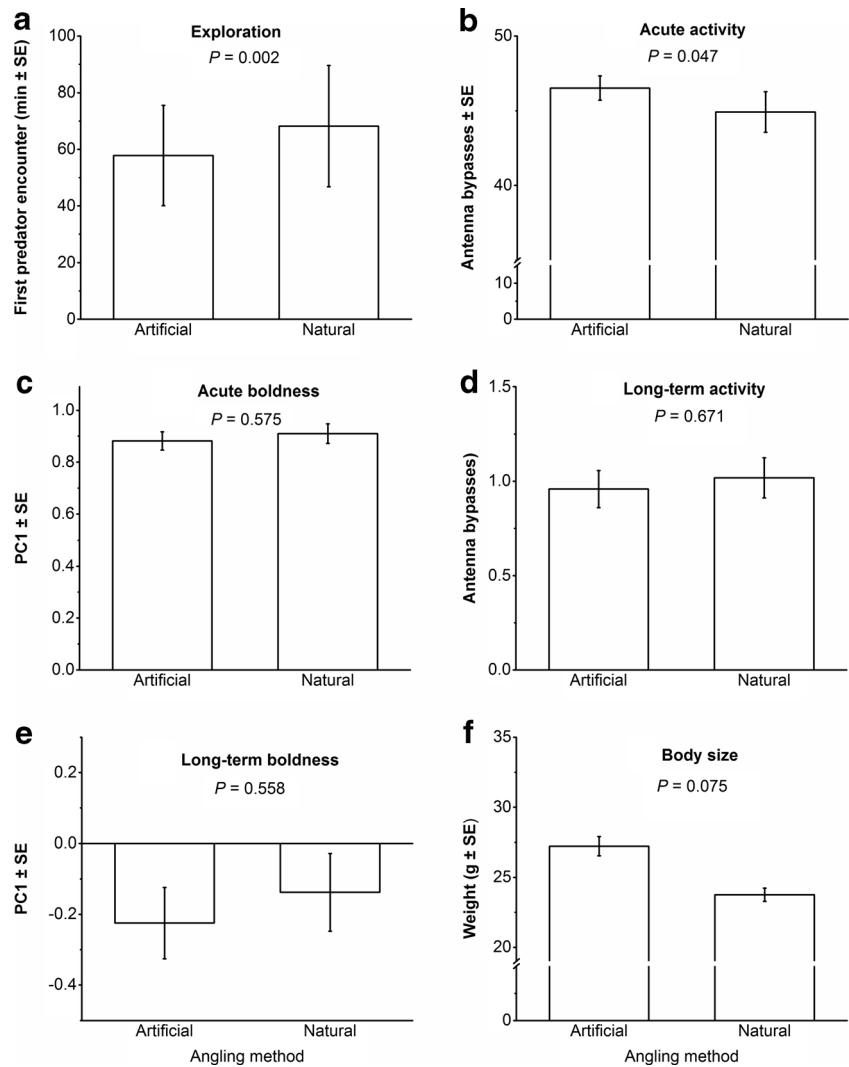
Variables that differ statistically significantly (GLMMs) between populations are written in italics

<sup>a</sup> Time to first predator encounter

<sup>b</sup> Mean daily antenna bypasses

<sup>c</sup> LN transformation used in analyses (mean values backtransformed in parentheses)

**Fig. 3** The observed differences in perch behaviour and size with respect to angling method (relative catchability groups): **a** Exploration, **b** acute activity, **c** acute boldness, **d** long-term activity, **e** long-term boldness and **f** body size



length ( $F_{1, 130.901}=2.480$ ,  $P=0.118$ ) or body condition ( $F_{1, 156.005}=1.180$ ,  $P=0.279$ ). The captured perch differed between populations in terms of body weight ( $F_{2, 52.556}=4.889$ ,  $P=0.011$ ) and body length ( $F_{2, 53.577}=4.719$ ,  $P=0.013$ ): the perch captured from Mieslahti Bay were the smallest both in terms of length and weight, whereas the perch from Lake Kivesjärvi were the largest in length and weight (Table 3). The body condition did not differ between populations ( $F_{2, 156.005}=0.827$ ,  $P=0.439$ ).

## Discussion

We found that the perch groups differing in relative catchability expressed distinguishable behavioural types under experimental conditions. Since perch were caught with natural method from several locations (16 %) where no fish were earlier captured using the artificial method, and more importantly, since the fish stopped showing interest towards an artificial lure, it can also be argued that the angling methods

differed in their efficiency to catch perch as predicted. In particular, the relatively inefficient artificial method applied first yielded perch with a high tendency to actively explore their environment (i.e. fast exploration and high acute activity), whereas the more efficient natural method used later was applicable to capture also the slow explorers and low-activity types. However, the fish did not differ in boldness or activity in the long term with regard to their relative catchability. Both methods captured fish of equal body size, demonstrating that the angling methods were not size-selective within the captured size range of fish. Despite significant population differences in mean size and behavioural measures, the links between fast exploration, high acute activity and relative catchability were present in all study populations, i.e. no interactions between populations and angling method were observed.

Wild perch exhibited repeatable between-individual variation in terms of activity and boldness in the experimental streams, thus confirming the results of Kekäläinen et al. (2014). In other words, differences in activity and boldness



among individuals were expressed consistently in both novel and familiar environment (i.e. throughout the experiment). Accordingly, bold individuals showing high risk-taking behaviour in the presence of predators often react by being less disturbed by predator presence, whereas shy individuals react to experienced predation risk by reducing their activity and seeking shelter (Sneddon 2003; Magnhagen 2006). However, the consistency of activity was found to be lower (16 % of the behavioural variation lied between the individuals) in comparison to boldness (44 %). The difference was due to an overpowering effect of within-individual variation in activity, i.e. substantial decrease in swimming activity within each individual subject as a response to habituation (Fig. 2).

Our study demonstrated that exploration behaviour had a more important role contributing to differences in relative catchability than behaviours expressed in familiar conditions (general activity, boldness). Since boldness is commonly coupled with explorative and active behaviours (Réale et al. 2007; Biro and Post 2008; Kortet et al. 2014), it was surprising that the consistent differences in boldness were not relevant for contributing to relative catchability. However, in any angling situation, the probability of a fish attacking the offered bait and hook may depend on its risk-taking tendency, whereas behavioural responses measured in a short-term setting in a novel environment usually provide essential data on risk-associated traits (Stamps 2007; Wolf et al. 2007). In particular, slow explorers have been found to take fewer risks than fast explorers (Stuber et al. 2013), and thus, the importance of exploration contributing to catchability seems reasonable. The importance of exploration behaviour on catchability is supported by Härkönen et al. (2014) who found that highly explorative behaviour in brown trout (*Salmo trutta*) increases the probability of an individual to become captured by angling. Wilson et al. (2011) reported that the bluegill sunfish (*Lepomis macrochirus*) caught using a seine net exhibit greater exploration compared to fish angled with a lure. Our results are also in line with those of Binder et al. (2012), who did not find differences in basal locomotory activity of largemouth bass selected for low or high vulnerability to angling. However, we cannot assess here whether explorative personality would directly contribute to vulnerability to angling in general. This is firstly because the extremely shy explorers were presumably not motivated to take either of the offered baits (see also Biro and Dingemanse 2009; Guillette et al. 2010) and secondly, because our experimental design did not allow us to assess the consistency of among-individual variation in exploration behaviour.

Capture order has been suggested to represent a relative measure of vulnerability to angling. For example, Vainikka et al. (2012a) found significant negative catch order effects on size variables in some perch populations, potentially arising from size-dependent dominance in feeding hierarchy (see also Tsuboi and Morita 2004). Kekäläinen et al. (2014)

conducted a study similar to ours, except that they focused only on a single population and used only the artificial or natural ice fishing gear at each fishing location. They found no capture order effects or between-method differences in perch behaviour or personality. On the contrary, our study showed that the combined change in lure type along the capture order amplified the selectivity on different behavioural phenotypes as assumed a priori. Although we cannot directly address the relationship between behaviour and capture order (irrespective of method) in this study, it is likely that the explorative perch captured first with the artificial lure would have been vulnerable to becoming angled early in the order with any method. Some individuals are more likely to lead the shoals in various conditions than the others (Burns et al. 2012; but see Krause et al. 2000), and the artificial lure used first may have targeted specifically the leading individuals. The active, explorative fish may have obtained a leading role within the natural shoals and maintained that role also in the experimental environment (see also Kekäläinen et al. 2014). In order to study whether individually consistent behavioural tendencies impact vulnerability to angling through the social hierarchies, more research on the impact of an individual's personality on shoal dynamics is needed using replicated and manipulated social environments.

The selectivity of the artificial method towards explorative and active behavioural types was present in all three study populations since no significant population by angling method interactions was found. However, the differences in the mean behavioural responses between populations were significant. Population differences in perch behaviour may lack heritable basis and arise mainly through environmental variation or experience (Hellström and Magnhagen 2011; Magnhagen et al. 2012). For example, bolder fish may be more likely to inhabit and feed in open water areas than shy fish, which generally avoid risky habitats (Wilson et al. 2011). Accordingly, observed differences may be due to differences in the sampled habitats between the populations. Perch from Martinlahti Bay, that showed on average the fastest exploration, the highest activity and the highest boldness scores through the long-term experiment, were captured from non-vegetated offshore habitats. The shyest fish in terms of all tested variables were captured from vegetated near-shore habitats in the eutrophic Lake Kivesjärvi. The observed population differences in behavioural patterns may thus have resulted from confounding interactions between fish personality and habitat use (as observed by Wilson et al. 2011), but we cannot address the direction of causality relationship in this study.

The artificial or natural method was not selective on fish size within the observed size range of fish. Earlier, high growth rate and high standard metabolic rate, in particular, have been reported to be central traits that may be selected against size-selective fisheries (e.g. Cooke et al. 2007; Redpath et al. 2009). Unfortunately, we were not able to

recover data for traits such as age and sex (because the fish were lost during the later experiments not described here), and the individual growth during the experiment was negligible for examining the relationship between behavioural and life history traits. In addition, the largest perch had to be excluded from the behavioural experiment excluding some potential size-related effects on behavioural variation. Nevertheless, we found that the explorativeness was not affected by any of the size variables indicating that exploration behaviour might contribute to relative catchability independently of body size. Instead, the best size-related predictor for acute behavioural variation in novel environment was the body weight, whereas in the long term, it was the body condition. Bold or active behaviours are often coupled with high foraging rate (e.g. Biro and Post 2008), but our results suggest that in high acute activity and acute boldness, the scores were coupled with small body size. On the other hand, long-term behaviour in a familiar environment may reflect an individual's intrinsic and state-dependent qualities, e.g. body condition or the motivation to feed, rather than personality (Tsuboi and Morita 2004; Philipp et al. 2009). Due to assumedly highest food density in the risky sections (see Fig. 1), high overall/long-term activity and boldness scores among fish in good condition likely reflected willingness to feed in the presence of a predator during the experimental period.

For future animal personality research, our study provides some good cautionary examples. First, it has already been recognised that it is not irrelevant how wild individuals are captured for behavioural studies (Biro and Dingemanse 2009; Wilson et al. 2011). According to our main results, different capture methods may be necessary when aiming for a representative sample to estimate behavioural variation of wild fish in experimental conditions. Second, a concern has been raised whether the expression of different behavioural types in laboratory conditions can be generalised into wider ecological or evolutionary contexts (Niemelä and Dingemanse 2014). We consider the behavioural types expressed under our experimental setting to represent relatively well those expressed in the wild because we used (1) enriched nature-like environment, (2) groups of fish as the individuals might have become stressed in isolation and (3) automatic behavioural surveillance when no stress was caused by human disturbance during the experiment. In addition, (4) our long-term setting allowed the fish to habituate to experimental settings. As a result, we found a strong habituation effect on the activity and boldness patterns over the course of the long-term experiment, i.e. it took several days for the wild perch to recover their normal activity levels after initial, probably partly stress-induced responses (e.g. due to handling).

Novel experimental approaches are still needed to identify potential consequences of individual differences in catchability in the context of group behaviour. Our study shows that combining both order effects and gear effects, the

fish show differences that could be explained by their tendency to occupy front position in a school. Both individual level studies with independent gear effects (see Kekäläinen et al. 2014) and group experiments are needed to link personality to group behaviour and to disentangle the effect of individual personality from group behaviour effects. Also, long-term behavioural experiments are needed to link individual growth with the development of behaviour in relation to body size and maturation (c.f. Niemelä et al. 2013). Of a particular interest, it would be to study if small body-sized fast explorers keep their high activity and boldness scores when they reach a higher age/size, or whether small individuals trade-off risk taking for faster growth.

In conclusion, we detected that certain behavioural traits may be directly associated with the catchability of Eurasian perch, and that highly explorative individuals are more common among fish that get easily caught in any given location compared to fish that are more difficult to catch. Our study contributes to the cumulating evidence on fishing-induced selection on fish behaviour and personality by showing that different methods used in recreational angling may catch certain behavioural types selectively. Our results also suggest that fast-moving anglers may selectively harvest only the most explorative personalities, and such effects are not only temporary and caused by non-repeatable hunger effects or such (see also Härkönen et al. 2014). Thus, our study has some implications also for the management of fisheries: using different fishing methods might ensure that no overall directional selection on behavioural types would generally occur.

**Acknowledgments** We thank the reviewers for their comments on the manuscript. Tomasz Podgomiak is gratefully acknowledged for his help in the study and the fishing trials and Tapio Laaksonen for his intensive help in building the PIT antennas for this study. Pekka Kurttila is acknowledged for kindly providing the baits used for free. This research has been supported by a project grant from the Emil Aaltonen Foundation. This work conforms to the current laws of Finland (permit number ESAVI/4356/04.10.03/2011).

## References

- Anonymous (2011) Recreational Fishing 2010. Finnish Game and Fisheries Research Institute, Helsinki. [http://www.rktl.fi/www/uploads/pdf/uudet%20julkaisut/Tilastot/tilastoja\\_7\\_2011.pdf](http://www.rktl.fi/www/uploads/pdf/uudet%20julkaisut/Tilastot/tilastoja_7_2011.pdf). Accessed 10 Apr 2013
- Arlinghaus R, Klefoth T, Kobler A, Cooke SJ (2008) Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. *N Am J Fish Manag* 28:123–134
- Arreguín-Sánchez F (1996) Catchability: a key parameter for fish stock assessment. *Rev Fish Biol Fisher* 6:221–242
- Binder TR, Nannini MA, Wahl DH, Arlinghaus R, Klefoth T, Philipp DP, Cooke SJ (2012) Largemouth bass selected for differential vulnerability to angling exhibit similar routine locomotor activity in experimental ponds. *Trans Am Fish* 141:1252–1259

- Biro PA, Dingemanse NJ (2009) Sampling bias resulting from animal personality? *Trends Ecol Evol* 24:66–67
- Biro PA, Post JR (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proc Natl Acad Sci* 105:2919–1922
- Bolger T, Connolly PL (1989) The selection of suitable indices for the measurement and analysis of fish condition. *J Fish Biol* 34:171–182
- Burns ALJ, Herbert-Read JE, Morrell LJ, Ward AJW (2012) Consistency of leadership in shoals of mosquitofish (*Gambusia holbrooki*) in novel and in familiar environments. *PLoS ONE* 7(5):e36567. doi: 10.1371/journal.pone.0036567
- Conrad JL, Weinersmith KL, Brodin T, Salz JB, Sih A (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J Fish Biol* 78:395–435
- Cooke SJ, Suski CD, Ostrand KG, Wahl DH, Philipp DP (2007) Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiol Biochem Zool* 80:480–490
- Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol Lett* 7:734–739
- Dingemanse NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J Anim Ecol* 82:39–54
- Guillette LM, Bailey AA, Reddon AR, Hurd PL, Sturdy CB (2010) Capture order is repeatable in chickadees. *Int J Comp Psychol* 23: 216–224
- Härkönen L, Hyvärinen P, Paappanen J, Vainikka A (2014) Explorative behavior increases vulnerability to angling in hatchery-reared brown trout *Salmo trutta*. *Can J Fish Aquat Sci* 71:1900–1909
- Hellström G, Magnhagen C (2011) The influence of experience on risk taking: results from a common garden experiment on population of Eurasian perch. *Behav Ecol Sociobiol* 65:1917–1926
- Kekäläinen J, Podgorniak T, Puolakka T, Hyvärinen P, Vainikka (2014) Individually assessed boldness predicts Eurasian perch's *Perca fluviatilis* behaviour in shoals, but is not associated with the capture order or angling method. *J Fish Biol* 85:1603–1616
- Kortet R, Vainikka A, Janhunen M, Piironen J, Hyvärinen P (2014) Behavioral variation shows heritability in juvenile brown trout *Salmo trutta*. *Behav Ecol Sociobiol* 68:927–934
- Krause J, Hoare DJ, Krause S, Hemelrijk CK, Rubenstein DI (2000) Leadership in fish shoals. *Fish Fish* 1:82–89
- Lewin W-C, Arlinghaus R, Mehner T (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Rev Fish Sci* 14:305–367
- Magnhagen C (2006) Risk-taking behaviour in foraging young-of-the-year perch varies with population size structure. *Oecologia* 147: 734–743
- Magnhagen C, Bunnefeld N (2009) Express your personality or go along with the group: what determines the behaviour of shoaling perch? *Proc R Soc Lond B* 276:3369–3375
- Magnhagen C, Hellström G, Borchering J, Heynen M (2012) Boldness in two perch populations—long-term differences and the effect of predation pressure. *J Anim Ecol* 81:1311–1318
- Mittelbach GG, Ballew NG, Kjølsvik MK (2014) Fish behavioral types and their ecological consequences. *Can J Fish Aquat Sci* 71:927–944
- Niemelä PT, Dingemanse NJ (2014) Artificial environments and the study of ‘adaptive’ personalities. *Trends Ecol Evol* 29:245–247
- Niemelä PT, Dingemanse NJ, Alioravainen N, Vainikka A, Kortet R (2013) Personality pace-of-life hypothesis: testing genetic associations among personality and life-history. *Behav Ecol* 24:935–941
- Nuttall M, Berkes F, Forbes B, Kofinas G, Vlassova T, Wenzel G (2004) Hunting, herding, fishing and gathering: indigenous peoples and renewable resource use in the arctic. In: Symon C, Arris L, Heal B (eds) Arctic climate impact assessment. Cambridge University Press, Cambridge, pp 649–690
- Philipp DP, Cooke SJ, Claussen JE, Koppelman JB, Suski CD, Burkett DP (2009) Selection for vulnerability to angling in largemouth bass. *Trans Am Fish Soc* 138:189–199
- Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev* 82:291–318
- Réale D, Dingemanse NJ, Kazem AJN, Wright J (2010) Evolutionary and ecological approaches to the study of personality. *Phil Trans R Soc B* 365:3937–3946
- Redpath TD, Cooke SJ, Arlinghaus R, Wahl DH, Philipp DH (2009) Life-history traits and energetic status in relation to vulnerability to angling in an experimentally selected teleost fish. *Evol Appl* 2:312–323
- Rodewald P (2013) Effects of broodstock origin, rearing environment and release method on post-stocking performance of Atlantic salmon. Doctoral dissertation, University of Helsinki, Finland. [https://helda.helsinki.fi/bitstream/handle/10138/40333/rodewald\\_dissertation.pdf](https://helda.helsinki.fi/bitstream/handle/10138/40333/rodewald_dissertation.pdf)
- Rodewald P, Hyvärinen P, Hirvonen H (2011) Wild origin and enriched environment promote foraging rate and learning to forage on natural prey of captive reared Atlantic salmon parr. *Ecol Freshw Fish* 20: 569–579
- Sih A, Bell AM, Johnson JC, Ziemba RE (2004) Behavioral syndromes: an integrative overview. *Q Rev Biol* 79:241–277
- Sneddon LU (2003) The bold and the shy: individual differences in rainbow trout. *J Fish Biol* 62:971–975
- Stamps JA (2007) Growth-mortality tradeoffs and ‘personality traits’ in animals. *Ecol Lett* 10:355–363
- Stamps J, Grootuis TGG (2010) The development of animal personality: relevance, concepts and perspectives. *Biol Rev* 85:301–325
- Stuber EF, Araya-Aioy YG, Mathot KJ, Mutzel A, Nicolaus M, Wiimenga JJ, Mueller JC, Dingemanse NJ (2013) Slow explorers take less risk: a problem of sampling bias in ecological studies. *Behav Ecol* 24:1092–1098
- Tsuboi J, Morita K (2004) Selectivity effects on wild white-spotted charr (*Salvelinus leucomaenis*) during a catch and release fishery. *Fish Res* 69:229–238
- Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R (2008) A behavioural perspective on fishing-induced evolution. *Trends Ecol Evol* 23:419–421
- Vainikka A, Koskimäki J, Niemelä PT, Kortet R (2012a) Composition of the Eurasian perch (*Perca fluviatilis*) catches in ice fishing: does capture order predict body size? *Fish Res* 115–116:24–30
- Vainikka A, Huusko R, Hyvärinen P, Korhonen PK, Laaksonen T, Koskela J, Vielma J, Hirvonen H, Salminen M (2012b) Food restriction prior to release reduced precocious maturity and improves migration tendency of Atlantic salmon smolts. *Can J Fish Aquat Sci* 69:1981–1993
- van Oers K, Sinn DL (2013) Quantitative and molecular genetics of animal personality. In: Carere C, Maestriperi D (eds) Animal personalities. University of Chicago Press, Chicago, pp 149–200
- van Wijk SJ, Taylor MI, Creer S, Dreyer C, Rodrigues FM, Ramnarine IW, van Oosterhout C, Carvalho GR (2013) Experimental harvesting of fish populations drives genetically based shifts in body size and maturation. *Front Ecol Environ* 11:181–187
- Wilson ADM, Binder TR, McGrath KP, Cooke SJ, Godin J-GJ (2011) Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis macrochirus*. *Can J Fish Aquat Sci* 68:749–757
- Wolf M, van Doorn GS, Leimar O, Weissing FJ (2007) Life-history trade-offs favour the evolution of animal personalities. *Nature* 447:581–584
- Ylönen H, Kortet R, Myntti J, Vainikka A (2007) Predator odour recognition and antipredatory response in fish: does the prey know the predator diel rhythm? *Acta Oecologia* 31:1–7