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Article

Facing different predators: adaptiveness of behavioral and morphological traits under predation

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Abstract

Predation is thought to be one of the main structuring forces in animal communities. However, selective predation is often measured on isolated traits in response to a single predatory species, but only rarely are selective forces on several traits quantified or even compared between different predators naturally occurring in the same system. In the present study, we therefore measured behavioral and morphological traits in young-of-the-year Eurasian perch *Perca fluviatilis* and compared their selective values in response to the 2 most common predators, adult perch and pike *Esox lucius*. Using mixed effects models and model averaging to analyze our data, we quantified and compared the selectivity of the 2 predators on the different morphological and behavioral traits. We found that selection on the behavioral traits was higher than on morphological traits and perch predators preyed overall more selectively than pike predators. Pike tended to positively select shallow bodied and nonvigilant individuals (i.e. individuals not performing predator inspection). In contrast, perch predators selected mainly for bolder juvenile perch (i.e. individuals spending more time in the open, more active), which was most important. Our results are to the best of our knowledge the first that analyzed behavioral and morphological adaptations of juvenile perch facing 2 different predation strategies. We found that relative specific predation intensity for the divergent traits differed between the predators, providing some additional ideas why juvenile perch display such a high degree of phenotypic plasticity.

Key words: behavior, morphological variation, *Perca fluviatilis*, perch, pike, predator-specific defenses, selective predation.

Predation is thought to be one of the main structuring forces in freshwater communities (e.g. Sharma and Borgstrom 2008), influencing not only species assemblage through selective predation but also the distribution and abundance of phenotypes within a population (e.g. Kishida and Nishimura 2005; Bell and Sih 2007; Heynen et al. 2014). Typically a prey faces multiple predators (Sih et al. 1998), which might differ in size (Scharf et al. 2000), density (Magnhagen and Heibo 2004), habitat use (Krupa and Sih 1998), diel activity (Turesson and Bronmark 2004), and/or hunting strategy

(Kishida and Nishimura 2005), imposing different predator-specific selection forces on the shared prey.

In single predator systems, a predator-specific defense would decrease a prey's vulnerability to predation (Krupa and Sih 1998; Sih et al. 1998). In contrast, facing equally abundant predators with different strategies, a more plastic and general defense might be advantageous (Krupa and Sih 1998; Sih et al. 1998). Many defense strategies bear costs, confronting the prey with time and/or resource allocation trade-offs (e.g. Steiner and Pfeiffer 2007). Individual

sticklebacks *Gasterosteus aculeatus* that behave less actively (Moodie et al. 1973) or more vigilantly (Godin and Davis 1995) are less likely to fall victim to predation, but simultaneously lose foraging opportunities. In Crucian carp *Carassus carassus* increased body depth, though effective against gape limited predators (Nilsson et al. 1995), was also found to reduce competitive abilities (Pettersson and Bronmark 1997). Throughout many fish species, different behavioral and morphological defense strategies have been described such as group living (Magenhagen and Bunnefeld 2009), shortened spawning ascents (Habrun and Sancho 2012), vigilance (Pitcher 1992), reduced activity (Bean and Winfield 1995), or seeking shelter (Magenhagen et al. 2012), armor (Vamosi 2002), spines (Zimmerman 2007), or increased body depth (Brönmark and Pettersson 1994; Abate et al. 2010). The variety of behavioral and morphological defenses were sometimes shown to compensate or augment each other (Steiner and Pfeiffer 2007). In goldfish *Carassius auratus*, deep bodied individuals displayed lower intensity of antipredator response than shallow bodied ones, thus individuals with morphological defenses exhibited less behavioral modification than those lacking such defenses (Chivers et al. 2007). However, selective predation is often measured on isolated traits in response to a single predatory species, but only rarely are selective forces on several traits quantified (e.g. Bell and Sih 2007; Holmes and McCormick 2009; Smith and Blumstein 2010; Pruitt et al. 2012) or even compared between different predators naturally occurring in the same system (e.g. Botham et al. 2006; Holmes and McCormick 2009). Comparing the fitness consequences of just 1 axis of variation may, however, overestimate the importance of 1 trait and lead to a fractioned view on the operating selective forces (Steiner and Pfeiffer 2007).

Eurasian Perch (*Perca fluviatilis* L.) is a common freshwater species throughout Europe (e.g. Thorpe 1977), where juveniles (like most fishes), suffer the highest predatory mortality during their first year (Sogard 1997; Huss et al. 2010). For juvenile perch, the 2 most common predators are adult perch and pike *Esox lucius* (Persson et al. 2003; Magnhagen and Heibo 2004), which differ in habitat use and hunting strategies (Turesson and Bronmark 2004). Although perch predators hunt and search actively (Christensen 1996), pike is a sit-and-wait predator, ambushing the prey from shelter (Bean and Winfield 1995). Juvenile perch were found to show consistent variation in morphology (Borcherding and Magnhagen 2008) and behavior (Magnhagen and Bunnefeld 2009). The evidence suggests individuals adapt their behavior to the experienced level of predation risk (Magnhagen and Borcherding 2008) and increase their body depth in the presence of pike (Eklöv and Jonsson 2007). However, to our knowledge, the relative selection advantages of morphological and behavioral traits with respect to predation have not yet been quantified, or even compared for different predators.

In the present study, we therefore measured behavioral and morphological traits in young-of-the-year Eurasian perch and compared their selective values in response to the 2 most common predators, adult perch and pike. Boldness toward a predator and morphological features describing the body shape were measured before groups of juvenile perch faced either a piscivorous pike or perch. To analyze the selective value of the different phenotypic traits, we compared the initial morphological and behavioral characteristics of the juvenile fish that survived with the characteristics of the juvenile fish that were preyed upon. In order to reduce size selective predation in our setup, we applied a relatively low prey–predator size ratio. This would suggest that morphological traits, like a slightly

deeper body should be of minor importance, despite indications that predators regularly prefer shallow bodied prey to reduce handling time. In contrast, behavioral defense strategies should then be of higher importance in our analysis, and we hypothesize relatively risk prone prey individuals to suffer higher mortality rates. As an actively searching and hunting predator like perch depends to a greater extent on the behavior of its prey, we finally hypothesize that adult perch would prey more selectively than the sit-and-wait predator pike.

Material and Methods

In July and August 2010, in total 152 young-of-the-year perch (total length, T_L, mean $\pm$ *SD*, 61.9 $\pm$ 6.3 mm; weight, mean $\pm$ *SD*, 2.1 $\pm$ 0.7 g) were caught by beach seining in a gravel pit lake near the city of Rees (51°46′N, 6°20′E), Germany. The fish were directly transported to the Field Station Grietherbusch of the University of Cologne nearby and stocked to an outdoor tank (1.8 m^3) to acclimate to captivity (6–12 days). Fish were fed daily with pre-frozen chironomid larvae (6% of total body mass). The adult piscivorous perch used as predators (T_L, mean $\pm$ *SD*; 231.5 $\pm$ 18.3 mm, N = 17) were caught in another gravel pit lake (51°45′N, 6°28′E) and were fed with fish daily. Predatory pikes (T_L, mean $\pm$ *SD*; 146.7 $\pm$ 14.9 mm, N = 5) were caught in a small oxbow near the laboratory, and fed daily with fish.

Experimental design

Before being handled all fish were sedated with MS222. The juvenile perch were measured, weighed and carefully placed on wet thin towel, laying on a carved piece of Styrofoam to prevent deformation. Using a digital camera perch were photographed together with a ruler and then randomly marked with an individual color code on the caudal fin. Subsequently, the juvenile fish were transferred to small aquaria to recover from narcosis (30 min) and assigned to groups of 4 in an experimental aquarium. Each group participated in 1 behavioral experiment, with 2 repeated observations (see below). After the behavioral observations were conducted, 4 groups of 4 perch each (16 individuals) were added to 1 outdoor tank (60 cm high, 0.47 m^2, 50% cover with artificial vegetation), containing a piscivorous pike or perch. As adult perch are more sensitive to handling than pike (personal observation), the adult perch were stocked to the outdoor tanks 10 days and the pikes 3 days prior adding the juvenile fish. During this time the predators were not fed, to reach a high hunger level. In total, 10 circular outdoor tanks with recirculation pumps were used (mean $\pm$ *SD*, 17.5°C $\pm$ 1.5°C, natural light regime), to set up 5 replicates per predator species. Aiming to examine the predator-specific selection for different behavioral and morphological phenotypes and to ensure the comparability between the replicates, prey size was chosen to result in a constant prey–predator size ratio (prey–predator size ratio, perch: mean $\pm$ *SD*, 0.30 $\pm$ 0.02; pike: mean $\pm$ *SD*, 0.39 $\pm$ 0.02), which was slightly higher for pike, because they are less gape size limited than perch (Nilsson and Brönmark 2000). The study was conducted in 4 successive experimental blocks (with 2 tanks stocked with fewer prey fish, 12 individuals instead of 16). During the tank treatments, the juvenile perch were fed twice per day equal to 15% body weight, which was equally distributed over the whole tank and food amounts were adjusted according to the remaining amount of fish in each tank. The tanks were checked every second day, visually counting the remaining prey fish and each treatment ended, when about 50% of the prey fish were consumed. Tank treatments were on

average ended after 11 days, recovering between 18.7% and 66.6% of the prey and all the predators alive (survival prey, perch: mean $\pm$ SD, 42.4 $\pm$ 15.5%; pike: mean $\pm$ SD, 49.9 $\pm$ 12.8%). After the experiments the juvenile fish were sacrificed with an overdose of MS222 and frozen for further morphological analyses. The perch and pike predators were released at the same location they were caught.

Behavioral experiments

The experimental aquaria were 100 L (85 $\times$ 42 $\times$ 34 cm), their bottom was covered with gravel and the water temperature was 20.8°C $\pm$ 1.2 °C (mean $\pm$ SD), while the light regime in the room was set to 13L:11D. One-third of each aquarium was used for the predator separated with a plastic net and the remaining part for the group of perch. An opaque plastic screen was placed close to the net, to prevent the juvenile fish habituating to the predator. Artificial vegetation and aeration was provided in the predator compartment and in the half of the space for the perch group that was furthest away from the predator. After each set of behavioral experiments, one-third of the water in each aquarium was renewed.

Prior to the behavioral experiments, the small perch were acclimatized to the aquarium for 2 days and fed daily with red chironomid larvae in the open area. On the third day, the behavioral experiments were conducted, during which juvenile fish were observed twice. Before each observation, the juvenile perch were enclosed by the opaque screen in the half of their section that also contained the vegetation. Chironomid larvae ($\sim$75 larvae, corresponding to 3% of the total fish weight) were poured into the open space produced between the net and the opaque screen and allowed to sink to the bottom. The observation started by lifting the opaque screen, making a large perch visible to the juvenile perch though the net. Each aquarium was observed for 10 min, in which an observer recorded 4 different activities for each individual fish: occurrence in the vegetation, occurrence in the open, feeding, and predator inspection. Thereby, feeding was defined as being oriented toward the bottom and attacking the food and predator inspection as being within 2 fish lengths distance of the net and being orientated exactly toward the predator. The activities were entered into a computer program, which recorded 1 behavioral unit every second. After each observation the opaque screen was put back next to the net. All behavioral experiments were conducted in the same way and with the same predator species, adult perch, so the behavior of all juvenile perch for the pike and the perch tank treatment was tested in the presence of adult perch.

Morphological analyses

For morphometric analysis 12 homologous landmarks (9 defined points to describe the outer shape, 2 for the pectoral fin and 1 for the eye, respectively) were digitized on the left side of each specimen using tpsDigit and tpsUtility software from Rohlf (available at: http://life.bio.sunysb.edu/morph/; NY, USA). All the following analyses were performed with Integrated Morphometrics Package (IMP) developed by Sheets (which is available at: http://www2.canisius.edu/~sheets/morphsoft.html; Buffalo, NY, USA). All specimens were transformed to the same baseline orientation and length, using IMP software CoordGen6 and nonshape variations were removed, using the Procrustes superimposition option of the IMP software. Using the software PCAGen6n, a PCA was conducted and PCA scores were computed for the pike and perch data, respectively.

PCAGen6n was also used to visualize the morphometric distinction along the selected PCA axes as vectors on landmarks.

Statistical analyses

The recorded behavioral data were used to calculate 7 behavioral variables: time spent in the open area, total time spent feeding, latency to start feeding, duration of the first feeding bout, activity (number of changes between open area and vegetation), latency until first change of habitat, and time spent with predator inspection. Behavioral consistency over the 2 observations for the 7 behavioral variables was analyzed with Kendall correlations, as the data were not normally distributed. Using a principal component analyses (PCA), the average behavior per fish over the 2 observations for the calculated behavioral parameters were combined to behavioral scores, reducing the number of behavioral variables but retaining the variation present in the recorded data. Two PCAs were conducted for the perch and pike treatment data, respectively.

Possible connections between the measured behavioral and morphological parameters [principal component 1 and 2 from the behavioral analysis (B-PC1 and B-PC2) and principal component 1 and 2 from the morphological analysis (M-PC1 and M-PC2)] were analyzed with Pearson correlations for the perch and pike treatment data, respectively. To analyze the factors influencing the survival of a prey individual, 2 separate linear mixed effect models were setup for perch and pike. Survival (0/1) was used as binominal response variable. To avoid pseudoreplication in the analysis, a nested design was created. "Between-groups in one tank" was added as random effect at the inner level and "between-tanks" was added as random effect at the outer level, to account for pseudoreplication (Hurlbert 1984). The following variables were added as fixed effects: principal component 1 and 2 from the behavioral analysis (B-PC1 and B-PC2), principal component 1 and 2 from the morphological analysis (M-PC1 and M-PC2), the average amount of prey consumed per day (PCPD) in each tank and the prey–predator size ratio (PPSR). Hence, the model for survival was fit with the predictors of PCPD, PPSR, Beahvioral-PC1, Behavioral-PC2, Morphological-PC1 and Morphological-PC2 without interactions and the random intercepts of group and tank ID.

The dredge function in the MuMIn package in R was used to run all possible combinations of the fixed effects and ranked the resulting models according to the associated AICs, to find the most parsimonious combinations of the fixed effects. Instead of focusing on a single minimum best model, the model.avg function in the MuMIn packed in R was used to average the models identified to best support our data (Johnson and Omland 2004), where models with Akaike difference < 2 were considered important (Burnham and Anderson 2002). Parameter estimates were averaged according to Akaike's weights. This resulted in robust parameter estimates and predictions, and helped to avoid to focusing on or rejecting a special hypothesis, where multiple alternative hypotheses may be relevant (Johnson and Omland 2004). This approach is especially useful, allowing us to identify and present the relative contributions of the different important factors in explaining our data.

Results

Behavior

For all 7 behavioral variables the behavior of the first and second observation were significantly positively correlated (for all 7 correlations $P < 0.01$; Kendall's tau coefficient range 0.28–0.57). For the

behavioral data from the juvenile fish used in the pike treatments, the PCA produced 2 behavioral principle components with eigenvalues > 1 (B-PC1 and B-PC2), explaining together 79.5% of the variation (Table 1). Whereas the PCA on the behavioral data from juvenile prey perch used in the perch treatments resulted in only 1 axes with an eigenvalue > 1 (B-PC1), however we retained the first 2 axes for comparability, explaining together 80.6% of the variation (Table 1).

The loadings on the 2 axes were similar between the behavioral data from the juvenile perch used in the different predator treatments, resulting in comparable scores, where positive scores on B-PC1 indicated more time in the open, more time feeding, a lower latency to start feeding, a higher activity (number of changes between open area and vegetation) and a lower latency to leave the vegetation, which would signify a fish with a high degree of boldness. Positive scores on B-PC2 indicated more time spent with predator inspection and a lower duration of the first feeding bout, signifying vigilance.

Morphology

From the 2 morphometric analyses, we retained the first 2 principal components for further analyses, explaining together 52.8% and 56.7% of the morphological variation between the juvenile perch used for the perch and pike treatments, respectively. The shape difference associated with the first morphological principal component (M-PC1) were similar for the pike and perch population subsamples, where positive scores on M-PC1 indicated a more downward bended body shape and a deeper bodied appearance (Figure 1). For the juvenile prey perch used in the perch treatments positive scores on M-PC2 indicate a larger head, whereas for the juveniles used in the pike treatments positive scores on M-PC2 are associated with smaller head morphology (Figure 1).

Neither for the perch nor the pike treatment data were any of behavioral parameters (B-PC1 and B-PC2) significantly correlated with the morphological parameters (M-PC1 and M-PC2) ($P >$ 0.05; Pearson product–moment correlation coefficient range -0.15 to 0.20).

Mixed effect models—random effects

The variance (var) explained by the 2 random effects, "between-tanks" and "between-groups in one tank," was close to zero (var < 1.0^{-5}) in both the most parsimonious perch as well as the most parsimonious pike treatment model.

Mixed effect models—fixed factors

Testing for the most parsimonious combinations of fixed effects resulted in 7 models with Akaike differences < 2 per predator model, including a mean of 2 terms for the models for the perch data and 0.85 terms for the pike models, respectively (Table 2). Multimodel inference from the subsets of important models indicates that only the fixed factor behavioral component 1 (B-PC1 boldness) showed a trend different from zero (Table 3). This is also reflected by the relative variable importance of the fixed factors, indicating that between individual variation in behavioral component 1 (B-PC1 boldness), but also variation in behavioral component 2 (B-PC2 vigilance) and morphological component 1 (M-PC1 body shape) contribute to the likelihood that a juvenile perch is preyed upon in a perch treatment (Table 3, Figure 2). For the pike treatments, all examined factors had a relative low contribution in explaining the survival of prey individuals, among which the between individual variation on behavioral component 2 (B-PC2 vigilance) seems to be most important (Table 3, Figure 2).

Discussion

In the sets of the most parsimonious models, the numbers and combinations of the fixed effects differed between the pike and the perch data. The most parsimonious pike models contained zero or only 1 fixed effect, however without any consistency. In contrast, the best perch models contained on average more fixed effects and the factor boldness appeared consistently in all models. Consequently, the fixed effect boldness had the highest relative variable importance in the perch models, in which between individual prey variation in boldness was negatively related to survival. These results indicate that perch predators preyed selectively on bolder juvenile perch and overall considerably more selectively than pike.

We kept size variation between the prey individuals small in the present study, to focus purely on the effects of morphological and behavioral variation. In consequence, the prey–predator size ratio and accordingly size selective predation was of only minor importance. Size-biased predation is, however, a common phenomenon in fish populations (Juanes and Conover 1994; Lundvall et al. 1999). It may be attributed to gape limitations, in which a fish's vulnerability to predators changes with size (e.g. Lundvall et al. 1999) and body depth (e.g. Nilsson and Brönmark 2000), but may also result from size associated variation in preys escape ability (e.g. Taylor and McPhail 1985), conspicuousness (e.g. Lundvall et al. 1999), or behavior (e.g. Biro et al. 2004). For example, larger prey individuals might suffer from increased mortality, because they allocate their time in the trade-

Table 1. Factor loadings, eigenvalues, and proportion of the total variance explained by the first behavioral principle components (B-PC) extracted from the 2 PCAs over the 7 different measures of behavior, for the perch and pike treatments, respectively

|	Perch		Pike	
	B-PC1 Boldness	B-PC2 Vigilance	B-PC1 Boldness	B-PC2 Vigilance
Time in the open	**0.402**	0.211	**0.426**	−0.041
Total time spent feeding	**0.403**	−0.340	**0.407**	−0.342
Latency to start feeding	**−0.424**	0.038	**−0.439**	−0.097
Duration of first feeding bout	0.318	**−0.523**	0.362	**−0.406**
Number of changes	**0.403**	−0.063	**0.384**	0.268
Time spent with predator inspection	0.256	**0.725**	0.060	**0.748**
Latency until first change	**−0.405**	−0.185	**−0.418**	−0.271
Proportion of total variance	0.693	0.113	0.598	0.196
Eigenvalue	4.848	0.790	4.190	1.375
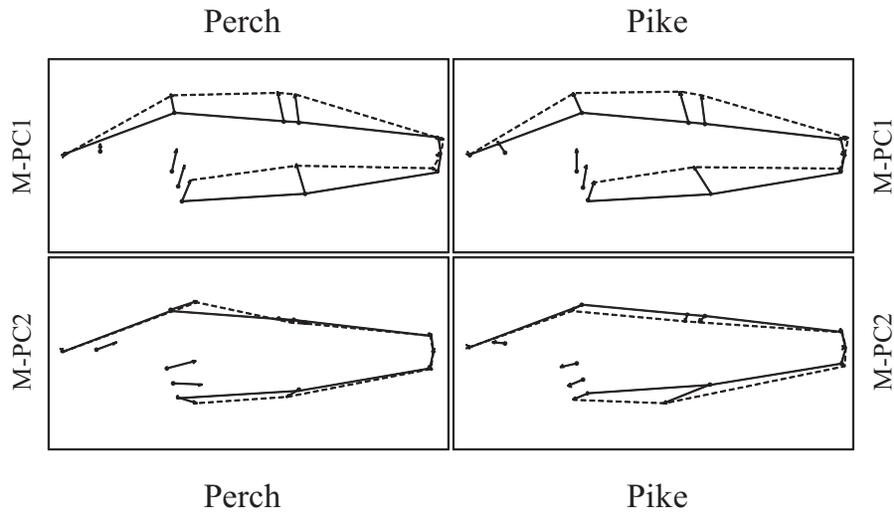
Figure 1. Shape difference associated with the first and second morphological principle component (M-PC1 and M-PC2) from the juvenile perch that participated in the perch and the pike tank treatment. The shape differences are depicted as growth vectors starting from the perch with small M-PC scores (solid line) to the perch with high M-PC scores (dotted line).
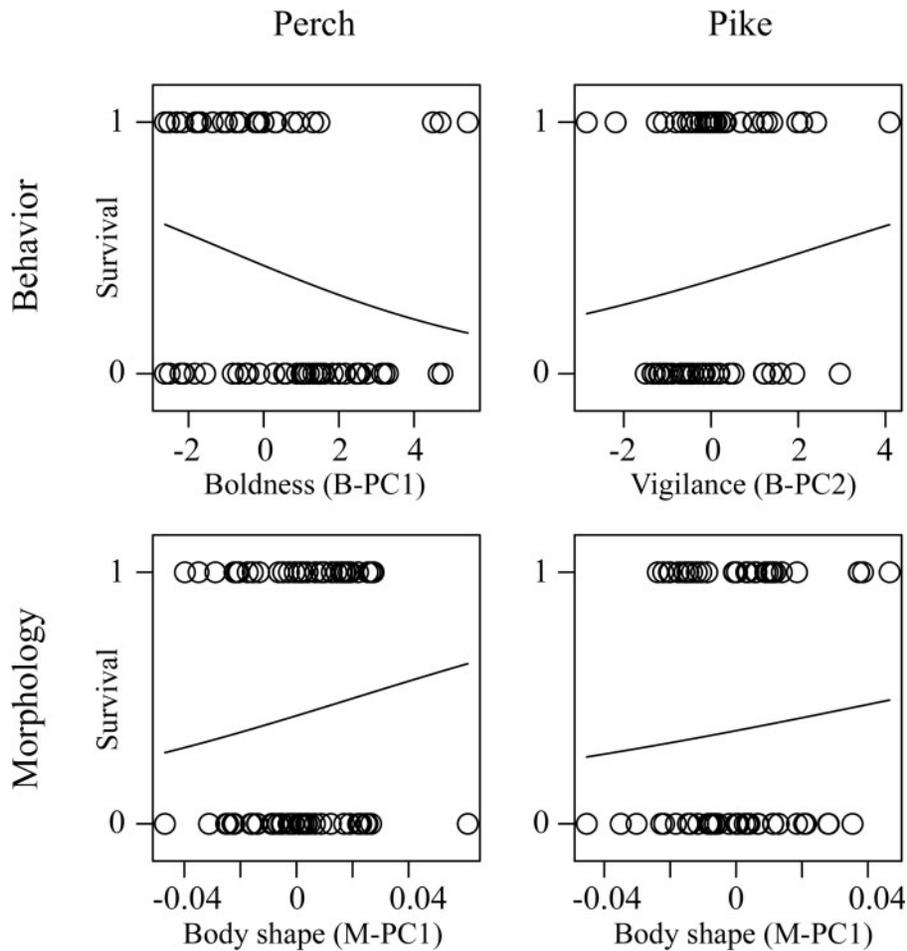

Figure 2. Vulnerability function for the divergent behavioral (B-PC1 and B-PC2) and morphological (M-PC1) phenotypes in response to adult pike and perch, extracted from the averaged model for pike and perch treatment data. On the *Y*-axes 1 indicates survival and 0 nonsurvival (death through predation). Multimodel inference indicate that only the behavioral component 1 (B-PC1 boldness) shows a trend different from zero.

Table 2. Akaike weights (ω_i), Akaike differences (Δ_i), Akaike information criteria, k values and the terms [behavioral component 1 and 2 (B-PC), morphological component 1 and 2 (M-PC), prey consumed per day (PCPD), and the prey-predator size ratio (PPSR)] and associated co-efficients in each model for the perch and pike treatment models

	Intercept	B-PC1 Boldness	B-PC2 Vigilance	M-PC1 Body shape	M-PC2 Head size	PCPD	PPSR	k	AIC	ΔAIC	AIC weight
Perch	−0.328	−0.246						4	112.0	0.000	0.098
	−0.332	−0.258		13.91				5	112.8	0.811	0.065
	−0.332	−0.242	−0.301					5	102.9	0.885	0.063
	−0.328	−0.252			15.04			5	113.4	1.416	0.048
	−0.335	−0.255	−0.293	13.57				6	113.7	1.740	0.041
	−0.527	−0.263				0.147		5	113.8	1.815	0.039
	0.391	−0.247					−2.39	5	114.0	1.975	0.036
Pike	−0.111							3	105.6	0.000	0.094
	−0.112		0.221					4	106.4	0.847	0.061
	−3.834						9.39	4	106.9	1.282	0.049
	−0.113			10.68				4	106.9	1.356	0.047
	0.453					−0.912		4	107.0	1.425	0.046
	−0.112				−11.18			4	107.2	1.561	0.043
	−0.111	0.032						4	107.5	1.925	0.036

Table 3. The coefficient, standard error, lower and upper 95% confidence interval, and the relative variable importance (Rel var importance) for each term [behavioral component 1 and 2 (B-PC), morphological component 1 and 2 (M-PC), prey consumed per day (PCPD), and the prey–predator size ratio (PPSR)] of the averaged model for pike and perch treatment data

		Coefficient	SE	Lower CI	Upper CI	Rel var importance
Perch	Intercept	−0.283	0.679	−1.640	1.070	
	B-PC1 Boldness	*−2.251*	*0.114*	*−0.479*	*−0.023*	**1.00**
	B-PC2 Vigilance	−0.079	0.155	−0.384	0.226	0.27
	M-PC1 Body shape	3.740	7.140	−10.300	17.800	0.27
	M-PC2 Head size	1.850	4.560	−7.140	10.800	0.12
	PCPD	0.014	0.050	−0.084	0.114	0.10
	PPSR	−0.223	1.620	−3.450	3.000	0.09
Pike	Intercept	−0.531	1.240	−2.970	1.910	
	B-PC1 Boldness	0.031	0.116	−0.200	0.264	0.10
	B-PC2 Vigilance	0.221	0.209	−0.196	0.637	**0.16**
	M-PC1 Body shape	10.700	13.400	−16.000	37.400	0.13
	M-PC2 Head size	−11.200	16.900	−45.000	22.600	0.11
	PCPD	−0.912	1.210	−3.320	1.490	0.12
	PPSR	9.390	11.100	−12.800	31.600	0.13

off between feeding and antipredator behavior to maximize growth (Biro et al. 2004). These findings are in correlation to our results that revealed relatively bolder juvenile perch (i.e. spending more time in the open, more active) are less likely to survive during the perch treatments. These results are consistent with previous studies on three-spined sticklebacks *Gasterosteus aculeatus*, in which individuals that were more active (Moodie et al. 1973) and fed more (Bell and Sih 2007) had a higher mortality risk. In meta-analyses across several species, Smith and Blumstein (2008) found bolder individuals to have an increased reproductive success, but a shorter life span due to selective predation. Boldness that decreases refuge use and increases activity, increases the risk to encounter and to attract primarily visual oriented predators (Martel and Dill 1995), increasing predation risk. Additionally, Turesson and Brönmark (2004) found that solitary perch predators need to separate single individuals from a school to successfully attack them. Therefore, bold individuals that more often occupy front positions (Ward et al. 2004) and keep greater distance from the school (Wilson et al. 1993), might be more vulnerable to predation. However, some studies on fish and other animals found bold individuals to have a higher likelihood to survive in the presence of

predators compared to shy (Réale and Festa-Bianchet 2003; Brown et al. 2005; Smith and Blumstein 2010). Furthermore, the relative selective advantage of a specific behavior might depend on the individual predator (Smith and Blumstein 2010) and its behavior (Pruitt et al. 2012).

In contrast to perch, pike predators in the present study did not selectively prey upon bold individuals. Perch were found to show consistent between individual differences in behavior across situations (Magnhagen 2006; Magnhagen and Bunnefeld 2009), indicating that fish behaving bolder in the presence of perch predators will also do so in the presence of pike predators. Nevertheless, it should be kept in mind that the initial behavior of all juvenile perch was tested in the presence of perch when interpreting predator-specific differences in selection on behavioral traits. Our results indicate a lower tendency for pike predators to hunt vigilant individuals that perform predator inspection. Although predator inspection is generally thought to increase an individual's vulnerability (e.g. Dugatkin 1992), Godin and Davis (1995) demonstrated that blue acaras (*Andinoacara pulcher* G., synonym *Aequidens pulcher*) as predators were less likely to attack guppies that inspected them than those that did not. In sticklebacks,

predator inspection was correlated with prey condition and escape ability (Kulling and Milinski 1992) and Pitcher (1992) suggested that predator inspections signals the predator that the prey is aware of its presence. Pike is a highly effective ambush predator (Eklöv and Diehl 1994; Bean and Winfield 1995; Turesson and Bronmark 2004), typically attacking its prey from a hideout in littoral vegetation. This tactic was suggested to be highly successful in piscivores because predators mostly attack unaware prey (Turesson and Bronmark 2004). However, this strategy might be less effective once detected by the prey, hence inspection might deter the predator from attacking (Pitcher 1992; Godin and Davis 1995).

Compared to the behavioral traits, selection on morphological traits was relatively low in the present study. Slightly downward bended individuals, with a deeper bodied appearance were more likely to survive than fish with a more slender appearance. Increased body depth is generally interpreted as an adaptive morphological prey characteristic that decreases a fish's vulnerability to gape size limited piscivores (e.g. Nilsson and Brönmark 2000). Indeed, Nilsson et al. (1995) could show that pike needs longer to process deep bodied Crucian carp and preferably attacks slender bodied individuals. We found pike predators to exhibit less morphological selection than perch predators. However, morphological variation in natural perch populations might be much more pronounced, suggesting that in the present study morphological variation might have been too small to be a selection criterion. Pike predators in the present study preyed less selectively than perch. Pike had a shorter starvation period and faced prey relatively larger than perch. Starvation is suggested to decrease selectivity in fish (Turesson et al. 2006), whereas increased relative prey size is assumed to pronounce morphological selection for shallow bodied prey in pike (Nilsson and Brönmark 2000). Hence, it might be suggested that the shorter starvation period and the higher prey–predator size ratio would rather increase selectivity in pike. This indicates that differences in selectivity between the divergent predators observed in our study are probably not an experimental artifact, but might be more pronounced under equal starvation levels. We found pike and perch to select differently on the different behavioral and morphological traits. Pike tended to positively select shallow bodied and nonvigilant individuals, whereas perch predators selected for shallow bodied and bolder juvenile perch. This supports the idea that different antipredator defenses may not be independent from each other (e.g. Lind and Cresswell 2005). In previous studies, different antipredator behaviors (e.g. Lind and Cresswell 2005), but also morphological and behavioral defense traits, were found to compensate or augment each other, depending on the ecological circumstances (Steiner and Pfeiffer 2007). For example, bolder *Radix balthica* (aquatic snail) exhibit a more defended shell shape than shy individuals (Ahlgren et al. 2015) and goldfish (Chivers et al. 2007), anural tadpoles *Rana pirica* (Kishida et al. 2009) and largemouth bass *Micropterus salmoides* (Brown et al. 2002) were found to decrease antipredator behavior with increasing body depth. However, we found no correlation between boldness, vigilance, and body depth for juvenile perch. Vigilance, that is predator inspection is generally interpreted as an act of boldness. In our study boldness (time in unsheltered habitat, activity, latency to leave the shelter) (as defined by e.g. Magnhagen and Borcherding 2008) and vigilance (predator inspection) were loaded on different PC axes, giving some evidence that they are not connected. Similar results were obtained in previous studies on juveniles from Swedish (Heynen et al. unpublished data) and German perch populations (Goldenberg et al. 2014), fathead minnows *Pimephales promelas* (Pellegrini et al. 2010) and

sticklebacks (Huntingford 1976). However, behavioral trait correlation or behavioral syndromes might also be species specific (Conrad et al. 2011). Our results on juvenile perch indicate that boldness and vigilance might represent uncorrelated alternative antipredator tactics, as suggested for shoaling and predator inspection in sticklebacks (Bell and Sih 2007). This is assumed to be advantageous for juvenile perch, as we found pike and perch to select differently on the 2 behavioral traits. Furthermore, defense strategies might bear costs, confronting the prey with time and/or resource allocation trade-offs (Steiner and Pfeiffer 2007). This can be also assumed in the present study, in which vigilance and shyness was associated with a lower foraging rate, as watching out for potential threats, inactivity, hiding and foraging are largely incompatible (e.g. Lind and Cresswell 2005). In previous studies, fishes were found to display a high degree of phenotypic plasticity (e.g. DeWitt and Scheiner 2004; and references therein). Juvenile perch were found to adapt their behavior on a long-term basis to the experienced level of predation risk (Magnhagen and Borcherding 2008; Magenhagen et al. 2012), but also to short-term changes of predation risk (Bean and Winfield 1995), by reducing activity and foraging, while intensifying the use of shelter. Furthermore, juvenile perch were found to increase in body depth in the presence of pike (Eklöv and Jonsson 2007). Hence, the results of the present study indicate that these plastic reactions are adaptive and might decrease an individual's vulnerability to predation. This might be particularly advantageous in the natural environment, where predation risk is not a fixed constant factor (Lima 2002). Predation risk for juvenile perch is expected to be variable due to population size structure, density and distribution of pike and adult perch, and might change through harvesting (Lewin et al. 2006), natural population circles (Persson et al. 2003), and/or interactions between predators (Eklöv and Diehl 1994). In a recent study, Svanbäck and Persson (2009) suggested that the intrinsically driven population dynamics in perch may favor morphological plasticity in perch over genetic diversification. Bearing in mind the results of the present study, that is that the 2 most common predators select with different intensity on different traits, clearly supports the idea of Svanbäck and Persson (2009). Thus, our results give some further hints, that not only the specific behavioral or morphological phenotypic reactions that individuals were found to display in response to predator risk (e.g. Bean and Winfield 1995; Eklöv and Jonsson 2007; Magnhagen and Borcherding 2008), but also the intrinsic ability to respond plastically to predation risk might be adaptive for perch (Svanback and Persson 2009; Kishida et al. 2010). Predator induced selection is suggested to effect the evolution of behavioral traits and wild populations of three-spined sticklebacks (Dingemanse et al. 2009), minnows *Phoxinus phoxinus* (Magurran 1986), and Trinidadian guppy *Poecilia reticulata* (Templeton et al. 2004) with differential predator regimes were found to differ in their antipredator behavior. The juvenile perch in the current study stem from a pike sympatric population and future studies including pike sympatric and naïve populations would help further elucidate the effects of multiple predator systems on the evolution of behavioral traits.

In conclusion, our results emphasized the importance of looking at more than 1 predator and more than 1 trait (e.g. Kishida and Nishimura 2005; Steiner and Pfeiffer 2007). This is mainly due because relative specific predation intensity for the divergent traits differed between the predators, in which the positive selection of perch predator on bold individuals was the most important. Thus, the results of the present study support the assumption that behavioral and morphological reactions of juvenile perch in response to a

predator might be advantageous, as it was suggested in several previous studies (e.g. Eklöv and Jonsson 2007; Magnhagen and Borcherding 2008). Furthermore, our results are, to the best of our knowledge, the first that analyzed behavioral and morphological adaptations of juvenile perch facing 2 different predation strategies. We provide some additional ideas as to why juvenile perch display such a high degree of phenotypic plasticity.

Acknowledgments

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