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Absence of a Context-General Behavioural Syndrome in a Solitary Predator

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Abstract

The correlation of seemingly unrelated behaviours into behavioural syndromes has been established in a wide range of species and taxa. However, most studies report on short-term behavioural correlations without insight into individual consistency or temporal stability of the behavioural syndrome. Here, we examine the individual repeatability of single behaviours, and the presence and temporal stability of a context-general behavioural syndrome in a solitary piscivorous predator, the pike (*Esox lucius*). Behavioural measurements on the same individuals were quantified independently through time and across three contexts: activity in the presence of a competitor, exploration of a novel environment and boldness under predation risk. There was no indication of a temporally stable behavioural syndrome, consisting of boldness, activity and exploration, nor were individuals consistent in the separate behaviours, contradicting the general assertion of its taxonomic prevalence. Furthermore, the study did not provide support for size or growth-dependent behaviour in this size-dimorphic species in conditions of limited food availability. The study highlights the importance of independent multiple observations of individual behaviour across time or contexts when measuring behavioural repeatability and covariation.

The occurrence of animal personalities, where individuals in a population vary consistently in their behaviour through time or across contexts, has been reported in a wide range of species and taxa (Gosling 2001; Sih et al. 2004a; Bell et al. 2009). In personality studies, the focus is often on the covariations of different behaviours, either across situations within a context (e.g. within a feeding context under different levels of predation risk) or across different contexts (e.g. feeding, mating), defined as context-specific and context-general behavioural syndromes, respectively (Sih et al. 2004a,b; Reale et al. 2010; Stamps & Groothuis 2010a). Within a syndrome, each individual exhibits a behavioural type, which is then either single-contextual, such as bolder vs. less bold types, or multiple-contextual, such as bolder and more aggressive vs. less bold and less-aggressive types (Bremner-Harrison et al. 2004; Sih et al. 2004a; Stamps & Groothuis 2010b). The latter is considered to have strong evolutionary implication, as it implies the co-evolution of functionally distinct individual behaviours (Stamps 1991; Sih et al. 2004a).

Associations between boldness, exploration and aggression constitute the most commonly reported context-general behavioural syndromes, and although positive correlations between these different behaviours are generally reported (Bell 2007; Smith & Blumstein 2010; Conrad et al. 2011), both species- and population-specific deviations have been reported. Studies on stickleback *Gasterosteus aculeatus* have been particularly revealing, showing that behavioural syndromes vary between populations (Bell 2005) and tend to only manifest in the presence of predators (Dingemanse et al. 2007). This variation has also been shown to have an inheritable basis (Dingemanse et al. 2012). It should be noted that most studies on behavioural syndromes have tested the different behaviours within the same day or over a small number of consecutive days. Such short-term behavioural correlations are frequently assumed to signify longer-term patterns without insight into individual consistency or ontogenetic stability of the behavioural syndrome (Sinn et al. 2010). Behavioural variables that are consistent for individuals over time represent reliable measures of the behavioural type they constitute (e.g. Jones & Godin 2010). Whilst repeatability of single individual behaviours therefore contributes to the stability of the behavioural type (Logue et al. 2009), composite scores summarise behaviours within a context and can be used to study behavioural correlations across contexts and consequently to detect the presence of behavioural syndromes (Bell 2005; Dingemanse et al. 2007; McGhee & Travis 2010). The importance of individual consistency of the single behavioural measures for the strength of behavioural syndromes has recently been raised (Logue et al. 2009; Stamps & Groothuis 2010a), with some concern over behavioural syndromes that lack the demonstration of individual stability being spurious (Logue et al. 2009).

Studies on context-general behavioural syndromes have tended to focus on species that have social traits such as parental care or dominance structures (Sih et al. 2004a; Reale et al. 2007; Conrad et al. 2011). Thus, the detection of behavioural syndromes in solitary animals has rarely been documented, and so the general view of the scope of behavioural syndromes could be biased. Pike *Esox lucius* is a solitary predator with a despotic-type distribution as a consequence of competitive exclusion through agonistic behaviour, such as cannibalism and kleptoparasitism (Nilsson & Bronmark 1999; Hawkins et al. 2005). Individual differences in wild pike populations have been noted for their habitat use (Knight et al. 2008), movement (Kobler et al. 2009) and migration from nursery habitats (Mann & Beaumont 1990; Cucherousset et al. 2009), which may be underlined by their behavioural types. Although the majority of theoretical models explain the occurrence of individual behavioural consistencies by differences in individual state (e.g. body size and age; Wolf & Weissing 2010), few empirical studies exist that have explicitly tested this (Dingemanse & Wolf 2010). As pike can display significant size dimorphism with, for example, a 60% difference in mean size attained between slow- and fast-growing individuals at the end of their first year of life (Mann & Beaumont 1990), it is an excellent model species to explore size-dependent behavioural syndromes. In this study, the presence of a context-general behavioural syndrome and its effect on individual growth rate and body size in juvenile pike is tested. It is hypothesised that (1) individual pike will behave consistently within the behavioural contexts over time; (2) pike will exhibit a context-general behavioural syndrome where bold individuals take consistently increased risk in predator presence, show higher aggression towards a competitor and have increased exploration rates in a novel environment; and (3) under limited food supply, the bold/aggressive/exploratory (multicontext) behavioural type is positively correlated with growth rate or/and body size.

Material and Methods

Collection of Study Fish

Young-of-the-year pike (47–74 mm fork length) were collected in a tributary of the River Frome, Dorset, UK, (50°419′N; 2°119′W), between 26 and 28 May 2010 by hand netting. The pike were immediately transported to aquarium facilities in 30-l buckets containing river water and air stones attached to battery operated air pumps to ensure sufficient oxygen levels. After acclimatisation to ambient temperature (16°C) of the laboratory for a minimum of 12 h, the pike were individually placed in 25-l glass aquaria (32 × 30 × 26 cm high) with continuous aeration and plastic plants for habitat enrichment. A 14 L:10 D photoperiod was maintained in the laboratory simulating the natural photoperiod. Three sides of the aquaria were covered with black plastic to prevent visual contact between individuals. The fish were fed with evenly sliced earthworm (*Dendrobaena veneta*) once per day by hand. The feeding procedure consisted of giving sequential portions of five slices, and new slices were added only if the previous portion had been eaten. Feeding continued for a maximum of 2 h, after which the remaining food items were collected. As juvenile pike have been shown to feed throughout the day with the greatest intensity at night (Ziliukiene & Ziliukas 2006) together with high evacuation rates of ingesta (Kaushik et al. 1985), a feeding time of 2 h during the daylight was considered limited (Nyqvist et al. 2012). Pike of age 1 + (160–180 mm fork length) were used as predators in the experiments and were caught by electric fishing (Smith-Root LR-24 backpack) from the same site. These larger pike were kept individually in a 50-l glass aquarium (64 × 30 × 26 cm high) containing oxygen filtration and plant cover, and fed *ad libitum* with whole *D. veneta*.

Experimental Protocol

The choice of contexts, which best represent certain personality traits in a species of interest, require careful consideration of species-specific behaviours (Bell 2007; Toms et al. 2010; Conrad et al. 2011). Here, juvenile pike encounter strong predation and competitive pressure by conspecifics in their nursery habitats (Grimm 1981; Mann 1982). Thus, the trade-off between feeding to grow fast and avoid predation (due to piscivorous gape limitation) and anti-predator avoidance is essential for juvenile pike survival (Lehtiniemi 2005). In addition, boldness has previously been measured as repeatable foraging behaviour under predation risk in this species (Nyqvist et al. 2012). Whilst the general behaviour of pike is strongly motivated by food, competitor and/or predator pressures, an appropriate context to measure exploration was considered to involve hidden food in a novel environment. With intracohort competition thought to be strong in juvenile pike, measuring antagonistic acts (e.g. attacks) and proximity to a competitor (similar-sized pike) are indicative of aggression. Thus, the individual repeatability of single behaviours, and the presence and temporal stability of a context-general behavioural syndrome, is examined here through recording of repeated and independent behavioural measurements on the same individuals across three contexts (i.e. treatments): (1) exploration of a novel environment; (2) aggression towards a competitor (similar-sized conspecific); and (3) feeding under risk of a predator (larger conspecific).

In each experiment, 34 juvenile pike [initial body mass (BM), $W_i = 1.24 \pm 0.11$ g, mean ± SE] were used and defined as focal fish. Each individual treatment (1–3) was repeated four times at 5-d intervals (i.e. 12 trials across all three treatments) during which the 34 individuals were tested (34 assays). Each trial was completed over 2 d between 9:00 and 18:00 h. Therefore, there were intervals of 5–6 d between the exposures of an individual pike to different contexts. Individuals were starved for 24 h prior to experiments to ensure similar hunger levels.

The experimental protocol meant each focal fish was removed from their holding tank by scooping using a 0.5-l beaker and transferred to an experimental tank with the same temperature and oxygen levels as that of the holding tanks, and acclimatised for 30 min. Each assay using single fish lasted 10 min and was recorded using a digital video camera. The order of assessment (time and day) of individual pike in each trial was randomised. At the conclusion of the individual assays, the fish were placed back in their individual holding tanks by scooping, and the water in the experimental tank was replaced with fresh conditioned and aerated water. Each fish was weighed 2 d after the completion of each 'foraging under risk of a predator' trial. All trials were carried out between 20 June and 17 October 2010 (119 d). All videos were subsequently analysed blind with respect to fish identity and in a randomised order by the same person (MJN).

Behavioural context 1: exploration of a novel environment

The experimental tank (40 × 40 × 30 cm high), with a water depth of 10 cm, consisted of two equal-sized compartments; a 'simple side' without any features and a 'complex side' with five features consisting of plastic plants, rocks and a petri dish containing gravel and one slice of *D. veneta*. The two compartments were separated by a removable divider and after acclimatisation in the simple side (30 min), the divider was gently lifted half-way out of the tank enabling the fish to access the complex side. All sides of the tank were covered to prevent other visual stimuli. The camera was mounted over the 'complex' side of tank and recorded the behaviour of pike in the new area (top view). A grid (5 × 5 cm squares) was placed underneath the tank for quantifying fish movement from the videos. The following metrics were quantified (1) latency of the fish to move into the 'complex' side of the tank, (2) time spent in new area, (3) number of squares traversed and (4) latency to the first prey attack. Individuals that did not move into the new area were given latency times of 10 min so as not to remove the least explorative animals. Here, latency to emerge in a novel environment is termed 'exploratory behaviour' following frameworks by Reale et al. (2007) and Conrad et al. (2011). The use of a complex structural side as part of the experimental design has previously been used in studies of fish exploratory behaviour (e.g. Bell 2005; Smith et al. 2009; Jones & Godin 2010). No effect of time of day of the experiments was found on any of the behavioural variables measured in the focal fish (ANOVA, all $p > 0.05$) and was therefore not included in further statistical models.

Behavioural context 2: aggression towards a competitor

The experimental tank (30 × 20 × 20 cm high) with a water depth of 10 cm, contained a 1-l transparent glass beaker that was placed on one side of the tank. After the acclimatisation period (30 min), a competitor of similar size (±5 mm; conspecific) from the same population was placed into the beaker, and lateral filming commenced. All the other three sides of the tank were covered to prevent other visual stimuli. From the videos, the following metrics were quantified: (1) latency to attack the competitor (2) number of attacks at the competitor, (3) time within one body length of the competitor, and (4) time oriented towards the competitor. Individuals that did not attack the competitor were given latency times of 10 min so as not to remove the animals that were least likely to attack. A competitor was not used twice in a row. A total of 12 competitors were repeatedly used in the experiments. No effect of time of day of the experiments or competitor individual used was found on any of the behavioural variables measured in the focal fish (ANOVA, all $p > 0.05$) and was therefore not included in further statistical models.

Behavioural context 3: boldness in the presence of a predator

The experimental tank (40 × 40 × 30 cm high) was divided into two parts by a glass wall and a removable opaque divider. A larger pike (160–180 mm fork length, 'predator') was placed in one side of the tank (water depth 20 cm) to acclimatise an hour prior to the experiments and the focal fish in the other side (water depth 10 cm). The opaque divider was gently removed, and the focal fish was left for 5 min to detect the predator before the start of the experiment. The trial began when three slices of *D. veneta* were gently dropped along the middle of the glass divider towards the predator side. All the other sides of the tank were covered to prevent other visual stimuli. The camera was mounted above the compartment containing the focal fish (top view). Predator detection was evident from the videos with focal pike freezing while facing the predator, and all focal fish detected the predator prior to the start of the experiment. From the video recordings, the following metrics were quantified: (1) latency to first attack on prey, (2) number of prey attacks, (3) time within one body length of the predator and (4) time oriented towards the predator. Three predator pike were repeatedly used, and they were kept in their experimental tanks throughout the experimental day. Focal fish were assigned randomly to the predator fish. Individuals that did not attack prey were given latency times of 10 min so as not to remove animals least likely to attack prey. No effect of time of day of the experiments or predator individual used was found on any of the behavioural variables measured in the focal fish (ANOVA, all $p > 0.05$) and was therefore not included in further statistical models.

Data and Statistical Analysis

The specific growth rate (SGR) expressed as a change of weight over time of each individual pike was determined at intervals, and over the whole experimental period (119 d) using the following formula: $\mathrm{SGR} = [\ln(W_f) - \ln(W_i)]*100/t$, where W_i and W_f are the initial and final BM (g) of the individual, and t is the number of days between the weight measurements.

To assess among-individual variation, we calculated the coefficient of variation (CV, % = SD/mean * 100) for each behavioural measure of the four trials within contexts as well as for the overall SGR and BM.

Individual behavioural consistency was determined by calculating the repeatability of the different behavioural measures across the four trials of each experimental context. Repeatability (±SE and 95% confidence intervals) was calculated using linear mixed-effects models for Gaussian data and generalised linear mixed-effects models for count data, both with individual ID fitted as the random effect and the behavioural variable as the dependent factor (Nakagawa & Schielzeth 2010). The number of squares traversed, number of attacks at competitor and number of prey attacks (predator context) constituted 'count' data and were analysed using the Poisson multiplicative over-dispersion model fitted by PQL (penalised quasi-likelihood) estimation on the original scale. Latency to first attack (predator and competitor contexts) was log-transformed to attain normal distributions and analysed using the restricted maximum likelihood model. Both models use a randomisation procedure for significance tests. The repeatability analyses were conducted using the rpt function in the rptR package in R 2.12.1 (R development core team 2009). To compare repeatability estimates, we compared effect sizes and the 95% confidence intervals in addition to determining whether the confidence intervals overlapped with zero rather than basing inferences purely on p-values (Nakagawa 2004; Garamszegi 2006; Nakagawa & Cuthill 2007).

Separate principal component analyses (PCA) were used to summarise the behavioural measurements for each repeated trial into component scores. All four variables within each trial and context correlated and were included in the PCA. Bartlett sphericity tests were performed to determine the sampling adequacy of the correlation matrices (Budaev 2010). The significant p-values of the Bartlett's tests (Supplementary Information; Table S1) indicated that the qualities of the matrices were satisfactory to proceed with the PCA. In all trials of each context, the behavioural variables loaded onto one main principal component with an eigenvalue >1 (Kaiser–Guttman) that explained 42–82% of the variance in observed data (Table 1). This generated a total of four component scores for every individual in each of the three contexts. These scores were used to test for correlations across contexts over time. As component scores were not all normally distributed, the non-parametric Spearman's correlation ranking test (r_s) was used. In addition, the behavioural variables were averaged (mean) across the four trials for each context, and analysed for between-context correlations. Correlations between components scores, or mean behavioural variables, initial and final BM and SGR were also analysed. Finally, we tested the structures of the covariance matrices among the four trials within a context for equality and proportionality by conducting common principal component (CPC) analysis. We used the jump-up approach on the Flury hierarchy (Phillips & Arnold 1999) with the programme CPC (Phillips 1998). Equality of the covariance matrices between the trials indicates temporal stability of the separate behaviours and allows conducting repeatability analyses on the component scores to assess individual consistency of the single behavioural types. Proportionality reveals a relationship between the covariance matrices where they share identical eigenvectors but eigenvalues differ by a proportional constant. Furthermore, inequality or non-proportionality between covariance matrices prohibits the performance of a wider PCA, where the trials of each context are pooled (McGhee & Travis 2010). As an alternative to a wider PCA, each behavioural measure for each trial and context was standardised to a mean of zero and standard deviation of one. An average standardised value was then calculated over the four trials, and Spearman's correlations were performed between each of the four measures of each context across the individual fish.

The sequential Bonferroni procedure was used to adjust for multiple correlations. All behavioural variables were tested for normality using the Kolmogorov–Smirnov test and subsequently log-transformed where needed. These analyses were conducted in STATISTICA, version 7.0, (Statsoft Inc., Tulsa, OK, USA).

Results

The final BM of the individuals (n = 34) ranged from 1.4 to 14.3 g, with a mean (±SE) of 4.3 (±0.5) g displaying a CV of 57.5% (initial BM, 0.5–4.1 g, CV = 51.2%). There was a significant correlation between initial and final BM ($r_s = 0.72$, $p < 0.001$), indicating that individual rank-order in size was maintained through the experimental period. The mean (±SE) SGR was 0.77 (±0.04)% per day with a moderate CV of 27.3%.

Results from the behavioural tests showed high among-individual variation in most behavioural measures with an overall mean CV of 83% (Table 2). In the new area context, latency to enter and time in the new area decreased and increased, respectively, with trial, whereas the other measures varied slightly without a temporal association (Table 2a). The low CV for latency to prey attack, especially in the first trial, was due to few individuals attacking, and so most individuals had been assigned a latency of 10 min (Table 2a). Although individuals varied greatly in the time oriented towards the competitor (CV = 61–91%), the mean values decreased overall with time (Table 2b). In contrast, the time oriented towards the predator was lower in the first compared with the subsequent trials (Table 2c).

Within-Context Behavioural Repeatability and Stability

Repeatability analyses of individual behaviours within the 'presence of a predator' context (context 3) showed a significant individual consistency for latency to prey attack. However, even if the effect size was higher compared with all other measures, the lower 95% confidence interval overlapped with 0 for latency to prey attack (Table 3). No behavioural variables were significantly repeatable in either the novel environment or competitor contexts (contexts 1 & 2, respectively; Table 3).

The output from the CPC showed that the structure of the covariance matrices were not equal nor proportional (i.e. the null hypotheses of equality and proportionality were rejected) within any of the contexts (New Environment, equality: $\chi^2 = 254.542$, $p < 0.0001$, proportionality: $\chi^2 = 214.189$, $p < 0.0001$; Competitor, equality: $\chi^2 = 132.698$, $p < 0.0001$, proportionality: $\chi^2 = 116.563$, $p < 0.0001$; Predator, equality: $\chi^2 = 62.125$, $p = 0.0005$, proportionality: $\chi^2 = 50.701$, $p = 0.0038$).

Between-Context Correlations (Behavioural Syndrome)

No significant correlations were found between component scores of the different contexts across time when using the four repeated trials of each context separately (Table 4). Correlation analyses of mean behavioural measures between contexts did not reveal any significant associations either (after

Table 1: Principal component analyses component loadings for juvenile pike *Esox lucius* behavioural variables and total variance explained for each of the four trials in (a) new environment, (b) competitor and (c) predator contexts

		Trial			
Context	Behavioural measure	1	2	3	4
(a) New environment	Latency to enter	0.91	0.81	0.96	0.85
	Time in new area	−0.90	−0.88	−0.93	−0.90
	Number of squares traversed	−0.88	−0.79	−0.79	−0.85
	Latency to prey attack	0.27	0.86	0.94	0.79
	Cumulative%	62.51	69.86	82.49	71.96
(b) Competitor	Latency to attack competitor	−0.78	−0.83	0.81	0.81
	Number of attacks	0.43	0.61	−0.60	
	Time oriented towards competitor	0.87	0.57	−0.92	−0.88
	Time near competitor	0.66	0.60	−0.56	−0.53
	Cumulative%	49.64	43.62	54.17	57.31
(c) Predator	Latency to prey attack	−0.90	−0.95	0.93	−0.95
	Number of prey attacks	0.89	0.96	−0.90	0.97
	Time oriented towards predator	0.05	−0.03	−0.14	−0.20
	Time near predator	0.25	0.22	−0.33	0.04
	Cumulative%	41.78	47.04	45.19	47.13

Table 2: Mean behavioural measurements (±SE) and CVs of juvenile pike (n = 34) in each trial of the (a) new environment, (b) competitor and (c) predator treatment

	1		2		3		4	
Behavioural measures	Mean ± SE	CV (%)	Mean ± SE	CV (%)	Mean ± SE	CV (%)	Mean ± SE	CV (%)
(a) New environment								
Latency to enter (s)	482 ± 44.9	52	423.4 ± 37.7	51	434.1 ± 34.6	47	403 ± 38.3	52
Time in new area (s)	81.5 ± 26.9	184	103.5 ± 26.8	149	139.8 ± 30.9	129	151.1 ± 33.1	120
Number of squares traversed	2.9 ± 1	195	3.8 ± 1.2	176	7.7 ± 3	224	4.8 ± 1.2	139
Latency to prey attack (s)	595.4 ± 3.5	3	545.7 ± 22.6	24	485.6 ± 28.2	34	566.9 ± 15.4	15
(b) Competitor								
Latency to attack competitor (s)	119.1 ± 31.8	156	113.8 ± 35.4	176	184.2 ± 43.5	136	201.7 ± 40.1	109
Number of attacks	2.5 ± 0.5	107	1.3 ± 0.3	130	0.2 ± 0.1	240	0	0
Time oriented towards competitor (s)	212.3 ± 26.2	72	211.9 ± 22.8	61	156.2 ± 24	88	139.7 ± 23.2	91
Time near competitor (s)	310.3 ± 30.2	57	373.5 ± 28.5	43	372.2 ± 21.0	32	331.6 ± 32.4	54
(c) Predator								
Latency to prey attack (s)	392.4 ± 48.1	67	293.9 ± 50	98	374 ± 48.1	74	512.1 ± 37.5	39
Number of prey attacks	0.7 ± 0.25	186	1.2 ± 0.23	109	0.8 ± 0.2	145	0.3 ± 0.14	245
Time oriented towards predator (s)	287.1 ± 37.2	71	490.6 ± 23.6	28	459.6 ± 22.6	28	442.0 ± 31.4	38
Time near predator (s)	234.2 ± 36.2	85	430.3 ± 28.5	38	391.2 ± 32.1	47	364.7 ± 35.6	53

CV, coefficient of variation.

Bonferroni corrections), nor were any significant correlations detected between the averaged standardised values of each behavioural measure across the contexts (Supporting information; Table S2). As a consequence of the covariance matrices of the within-context trials being unequal (CPC result), further analyses using pooled trials was not justified.

Size- or Growth-Dependent Behaviour

None of the component scores correlated with SGR (after Bonferroni corrections), but significant correlations were found between the third exploration and aggression scores and initial BM (Table 4). Among correlations between the average individual behavioural measures

Table 3: The repeatabilities (*R*) of behavioural measures in juvenile pike *Esox lucius* (n = 34) within each experimental context: (a) new environment (b) competitor and (c) predator

Context	Behavioural measure	*R*	SE	% CI	p
(a) New environment	Latency to enter (s)	0.02	0.07	0.00–0.25	0.443
	Latency to prey attack (s)	0.00	0.15	0.00–0.51	0.875
	Number of squares	0.00	0.14	0.00–0.43	0.887
	Time in new area (s)	0.00	0.05	0.00–0.17	0.647
(b) Competitor	Latency to attack competitor (s)	0.05	0.06	0.00–0.20	0.253
	Number of attacks	0.00	0.11	0.00–0.33	0.701
	Time oriented towards competitor (s)	0.01	0.05	0.00–0.16	0.390
	Time near competitor (s)	0.00	0.05	0.00–0.16	0.709
(c) Predator	Latency to prey attack (s)	0.16	0.09	0.00–0.34	**0.036**
	Number of prey attacks	0.02	0.09	0.00–0.30	0.438
	Time oriented towards predator (s)	0.06	0.07	0.00–0.25	0.221
	Time near predator (s)	0.00	0.05	0.00–0.16	0.649

Linear mixed-effects models (rptR package in R, Nakagawa & Schielzeth 2010) with fish identity fitted as random effect and the behavioural measure as dependent factor were used for calculating repeatabilities, standard errors, 95% confidence intervals (CIs) and p-values. Significant ($p < 0.05$) p-value is shown in bold.

Table 4: Spearman's correlations between the component scores of the four repeated trials of each behaviour, initial body mass (BM) and specific growth rate (SGR) in juvenile pike *Esox lucius*

Trial	Context	Aggression	Boldness	Initial BM (g)	SGR (% day^{-1})
1	Exploration	0.02	0.01	−0.09	-0.51^{a}
	Aggression	1.00	−0.17	0.18	0.10
	Boldness	−0.17	1.00	−0.25	0.11
2	Exploration	−0.16	0.14	−0.06	−0.03
	Aggression	1.00	−0.18	0.08	−0.02
	Boldness	−0.18	1.00	0.31	0.04
3	Exploration	0.19	0.05	0.48^{b}	0.01
	Aggression	1.00	−0.04	0.53^{b}	0.00
	Boldness	−0.04	1.00	−0.07	0.04
4	Exploration	−0.02	0.30	0.37	0.15
	Aggression	1.00	0.26	−0.29	0.00
	Boldness	0.26	1.00	−0.23	0.02

$^{a}p < 0.05$ and $^{b}p < 0.01$ (significant correlation after the sequential Bonferroni procedure).

and body mass/SGR, a significant association was found between time in the new area and final mass (Table 5).

Discussion

No experimental evidence for the presence of single or multicontext behavioural types was found in juvenile pike. The relationships between the single behaviours differed between trials conducted over time within each context, indicating that individual behaviour was not temporally stable. Among the single behavioural measures, significant individual repeatability was only detected in the latency to prey attack within the predator context. As none of the individual PCA scores correlated across contexts, the prediction that a general contextual behavioural syndrome exists in juvenile pike can be rejected. Also, as few and sporadic associations between individual behaviour and body size or growth were detected, the experiments failed to find general support for size or growth-dependent behaviour in this size-dimorphic species.

Studies of personality most frequently report on the occurrence of repeatable behaviours and the presence of aggressive, bold or exploratory behavioural types. Although CVs reflect the level of among-individual behavioural variation, which contributes to the repeatability estimates, an account of CVs together with significant repeatabilities is rare in personality studies. Therefore, comparing our results on within- and among-individual variation in pike to other species has proven difficult. Indeed, among the increasing studies reporting the presence of individual consistency in aggression, exploration and boldness contexts, our study reporting on its absence may be considered unexpected. That the behaviours loaded differently on PC1 depending on the trial (equality was not attained among the covariance structures) indicate that the behaviours and the relationships among them were unstable through time. A model of Wolf et al. (2007) suggests that the evolution of personality traits is favoured by life-history trade-offs. Considering that the survival of juvenile pike in their natural nursery habitats is largely determined by the trade-off between feeding and predation avoidance (Engstrom-Ost & Lehtiniemi 2004; Lehtiniemi 2005), individual consistency in exploratory and aggressive

Table 5: Spearman's rank correlations between mean behavioural measurements and initial and final body mass (BM) in (a) new environment, (b) competitor and (c) predator contexts of juvenile pike *Esox lucius*

Context	Behavioural measure	Initial BM (g)	Final BM (g)	SGR
(a) New environment	Latency to enter (s)	−0.27	−0.18	0.09
	Latency to prey attack (s)	0.08	0.00	0.06
	Number of squares	−0.20	−0.20	−0.10
	Time in new area (s)	-0.39^a	-0.55^b	−0.14
(b) Competitor	Latency to attack competitor (s)	−0.12	−0.06	0.26
	Number of attacks	−0.08	−0.03	0.07
	Time oriented towards competitor (s)	−0.02	0.13	0.03
	Time near competitor (s)	0.32	0.12	−0.29
(c) Predator	Latency to prey attack (s)	0.17	0.43	0.45^b
	Number of prey attacks	0.19	−0.02	−0.11
	Time oriented towards predator (s)	0.25	0.08	−0.09
	Time near predator (s)	0.35	0.34	0.03

SGR, specific growth rate.

$^a p < 0.05$ and $^b p < 0.01$ (significant correlation after the sequential Bonferroni procedure).

behaviours (measured under limiting or no opportunity to feed, respectively) may not be present in this species. If the behaviour has no positive feedbacks (e.g. increased food intake or avoiding risks), which ultimately affect fitness or its proxies (e.g. survival, growth), there is no advantage for individuals to remain consistent in the behaviour (Wolf et al. 2008; Wolf & Weissing 2010). Furthermore, if fitness does not associate with consistent behavioural types, frequency-dependent selection of behavioural types is highly unlikely (Wolf & Weissing 2010), resulting in behavioural plasticity. Alternatively, exploratory or aggressive behaviours may not yet have developed positive feedback mechanisms in these juvenile individuals. Indeed, behavioural consistency may be associated with ontogenetic development. For example, in the African cichlid, *Steatocranus casuarius*, juveniles were not found to exhibit behavioural consistency, a contrast to the adults (Budaev et al. 1999). Findings by Conrad & Sih (2009) indicated that a behavioural type was unstable in juvenile steelhead *Oncorhynchus mykiss*. The experiences through ontogeny, such as predator presence, group composition and outcomes of intraspecific contests can significantly affect personality traits (cf. Budaev & Brown 2011). In addition, the directional change in the overall values of the behavioural measures over time indicated that learning of the competitor or predator being restrained or the presence and position of food in the novel environment may have occurred. Avoiding habituation and learning in multiple testing of the same individuals can be difficult (Martin & Reale 2008; Budaev & Brown 2011). Considering recent studies on *G. aculeatus* where a behavioural syndrome was established only in predator presence (Bell 2005; Dingemanse et al. 2007), a site-specific attribute may explain the absence of behavioural consistency and correlations in our study. Low consistency may also be a result of low mutation rates together with strong selection (Santiago 1998) removing most of the genetic variation in the population. Indeed, the pike population studied has been found to have low genetic variation (Bournemouth University, unpublished data).

In addition to the lack of individual behavioural consistency, the pike were also characterised by a lack of behavioural correlations between functionally different contexts, also indicating that there was no carry-over effect of the non-random experimental sequence. Here, the time interval between trials of the three contexts that were tested for correlations was 1 and 2 wks. In comparison, many other studies of behavioural syndromes have conducted the experiments on the same day (e.g. Bell 2005; Lee & Bereijikian 2008; Pronk et al. 2010). When tests are carried out close together in time, then it is possible that the reason why individuals behave consistently is that little has changed for the individual state (Nyqvist et al. 2012). For example, if a fish is hungry, this could influence both its exploratory and foraging behaviour, causing them to covary. Indeed, results from a meta-analysis by Bell et al. (2009) show that behaviours measured closer together in time had higher repeatability estimates. Therefore, the importance of independent multiple observations of individual behaviour across longer time period or contexts when measuring behavioural repeatability and covariation should be emphasised.

As a solitary, apex predator, pike differ from most species for which exploratory or aggressive behavioural types have been found. Aggressive behavioural types are obviously important in species that establish dominance hierarchies or defend territories (Snekser et al. 2009; Magellan & Kaiser 2010). In such species, the function of aggression has been studied in adults as a way to gain access to mates and the behavioural measurements included attacks against conspecifics. Exploratory types have been described, for example, in invasive species (Cote et al. 2010) or in species searching for new breeding sites (Bergmuller & Taborsky 2010). To pinpoint consistent individual differences in response to a conspecific or new environment in a highly predatory species, the presence of a feeding opportunity may be required.

The lack of both individual consistency and behavioural syndromes reported here have lead to the absence of association between behaviour and growth. In many other studies reporting on such an association in fish, the individuals have been kept in groups, thus allowing for effects of competition or dominance hierarchies to impact individual growth (e.g. Vøllestad & Quinn 2003; Adriaenssens & Johnsson 2010). The pike could not be kept in groups due to the risk of cannibalism (ethical reasons), and so this does suggest a competitive environment may be necessary to induce the association between growth and behavioural traits and syndromes. Notwithstanding, in the cannibalistic sibling dorada (*B. moorei*), growth differences among isolated fish were significant and were also related to their boldness and aggression (Baras & Lucas 2010). Where individuals are bolder, more active and aggressive, faster growth tends to be achieved through their higher feeding activity and so greater food intake rates (Stamps 2007). In contrast, empirical evidence from a number of species show that increased levels of activity is related to decreased growth rates (e.g. Koch & Wieser 1983; Rennie et al. 2005; Reinbold et al. 2009). Such a growth-foraging activity trade-off provides an alternative theory explaining growth- and size-independent consistent behaviour.

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Supporting Information

Additional supporting information may be found in the online version of this article at the Publisher's web-site:

Table S1: Results from Bartlett's sphericity tests and Kaiser–Meyer–Olkin (KMO) measure of sampling adequacy of the correlation matrix for each of the four trials in (a) new environment, (b) competitor and (c) predator contexts.

Table S2: Spearman's correlations of the averaged standardised raw behavioural measures across trials between (a) new environment and predator, (b) new environment and competitor and (c) competitor and predator contexts.