

# Shy trout grow faster: exploring links between personality and fitness-related traits in the wild

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In many animals, individual differences in behavior show remarkable consistency across situations and contexts (i.e., animal personality and behavioral syndromes). Studies on the association between personality traits and fitness-related measures in nature are, however, important to clarify the causes and consequences of this phenomenon. Here, we tested for correlations between 3 behavioral axes in brown trout (*Salmo trutta*) parr: exploration tendency, behavioral flexibility, and aggressiveness. Next, we tested how these individual behaviors relate to social dominance and performance under natural conditions (growth, survival, and movement). We found support for behavioral syndromes in brown trout with less explorative individuals being less aggressive and showing more flexible behavior. In addition, these low-explorative personality types grew faster than bolder conspecifics in the wild. Standardized aggression in the laboratory was a poor indicator of social dominance, and neither of these 2 traits affected performance in the wild. These results challenge the view that personality traits can be predicted by constant associations with life-history trade-offs (e.g., boldness is linked with rapid growth). Moreover, our findings suggest that fitness predictions from laboratory measures of behavior should be made with caution and ideally tested in nature. *Key words:* aggressiveness and cryptic prey, animal personality, behavioral flexibility, behavioral syndrome, dominance, exploration tendency, life history, fitness. [*Behav Ecol*]

Individuals often display consistent differences in behaviors, so-called personality traits (Gosling 2001; Dingemanse and Reale 2005). Personality traits have now been identified in a variety of animal taxa from mollusks to mammals (for a review, see Gosling 2001 and Réale et al. 2007). The shyness–boldness continuum is so far the most studied aspect of personality, where some individuals repeatedly react cautiously to risks in the environment, whereas others respond in a bold manner (Wilson et al. 1994). Sometimes several personality traits associate and form correlated suites of behavior, often termed behavioral syndromes (Sih et al. 2004). For example, boldness is often associated with various other behaviors such as aggressiveness (e.g., Huntingford 1976) and exploration tendency (e.g., Bell 2005).

Some evidence suggests that personality traits are more plastic and can change with experience. Bold rainbow trout (*Onchorhynchus mykiss*), for instance, reduced their boldness after observing shy demonstrators (Frost et al. 2007). Furthermore, personality itself may affect how an individual adjusts its behavior by learning or habituation (further referred to as “behavioral flexibility”). However, the search for associations between personality traits and behavioral flexibility has yielded inconsistent results. Some work suggests that bold behavior aids animals in solving novel tasks (Dugatkin and Alfieri 2003; Sneddon 2003), whereas others show that shy, unaggressive individuals display more flexible behavior (for a review, see Koolhaas et al. 1999). Recent view is that repeated measures on the same individuals and more integrated analysis methods may help clarify patterns of association between personality and behavioral flexibility and reveal their ecological implications (e.g., Réale et al. 2007; Martin and Réale 2008; Dingemanse et al. 2010). Yet, data from wild pop-

ulations remain scarce (but see e.g., Martin and Réale 2008; Kontiainen et al. 2009; Minderman et al. 2009).

Although behavioral syndromes have been studied extensively, surprisingly little is known about the selective mechanisms by which they are maintained (Sih et al. 2004; Dingemanse and Reale 2005; Réale et al. 2007; Dingemanse et al. 2010). The benefits and costs associated with a specific behavior should be highly dependent on environmental conditions and may vary considerably during an individuals’ lifetime. It is therefore challenging to explain the occurrence of behavioral syndromes. However, several hypotheses have been recently proposed to explain the phenomenon (Dall et al. 2004; Sih et al. 2004; Dingemanse and Reale 2005; Wolf et al. 2007; Biro and Stamps 2008). First, it may simply be too costly to change strategy (constraint hypothesis, DeWitt et al. 1998; Bell 2005); for example, when a common controlling factor influences behaviors across contexts (e.g., hormones or genes with pleiotropic effects). Recent reports of genetic correlations between different personality traits provide some support for this view (van Oers et al. 2005; Nakayama and Miyatake 2010). Yet a growing body of evidence shows that personality traits can vary, often predictably, between developmental stages (Bell and Stamps 2004) and populations that differ in ecological conditions (Bell 2005; Dingemanse et al. 2007; Brydges et al. 2008; Herczeg et al. 2009). Behavioral syndromes may therefore reflect selection for combinations of behaviors that work well together in a certain habitat (adaptive hypothesis, Bell 2005). For example, stickleback populations under high predation pressure show a positive genetic correlation between boldness and aggression, whereas this correlation is absent in populations with a history of low predation pressure (Bell and Sih 2007; Dingemanse et al. 2007).

Why then do not all individuals behave in a similar consistent way? Evolutionary theory predicts that fluctuating selection pressures caused by environmental variation can help maintain trait variation (Burger and Gimelfarb 2002). Some support along this line has recently been reported for wild populations of great tit (*Parus major*) and red squirrels (*Tamiasciurus*

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Received 19 February 2010; revised 15 October 2010; accepted 17 October 2010.

*hudsonicus*) where environmental fluctuations changed both the strength and direction of selection on personality traits (Dingemanse et al. 2004; Boon et al. 2007).

Recent applications of game theory provide alternative adaptive explanations for personality traits. According to these ideas, variation in personality traits can be caused by a combination of frequency-dependent selection (Roff 1998) and individual differences in a “state variable” that generates different behaviors (Houston and McNamara 1999; Dall et al. 2004). State variables can represent any individual variation in physiological, behavioral, or morphological characters that have implications for behavioral payoffs (Houston and McNamara 1999). Several candidate state variables affecting personality traits have recently been suggested, including growth rate, size, skills, and experience (McElreath and Strimling 2006; Stamps 2007). Behavioral traits connected with these state variables are suggested to show the same variation and consistency as the state variable itself (Dall et al. 2004; Stamps 2007; Biro and Stamps 2008). For example, consistent individual differences in growth rate have been reported in nature (e.g., Ragland and Carter 2004; Johnsson and Bohlin 2006) indicating that individuals follow specific growth trajectories. On this basis, it has been assumed that individuals that prioritize fast growth should consistently be more willing to take risks (bold) and compete for food (e.g., aggressive, Stamps 2007). Ample support for the existence of such “high-risk, high-gain” phenotypes is available from studies on captive and/or domesticated animals (Biro and Stamps 2008), yet studies on wild populations are scarce and suggest more dynamic associations between personality traits and growth (Adriaenssens and Johnsson 2009).

In nature, salmonid fish show individual variation in behaviors such as space use (Armstrong et al. 1997), boldness (Sundström et al. 2004), foraging strategies (Bridcut and Giller 1995), and aggressiveness (Lahti et al. 2001). Some previous studies also suggest that dominance status can be associated with growth rate in nature (Höjesjö et al. 2004, but see e.g., Harwood et al. 2003) and that growth rate may be an important state variable influencing behavioral strategies in salmonid fish (Johnsson et al. 1996; Sundström et al. 2007).

Here, we investigate the association between individual behavior, dominance status, and performance in the wild in brown trout parr (*Salmo trutta*). Using a behavioral reaction norm approach (as discussed in Dingemanse et al. 2010), we measured individual variation in 3 components of brown trout behavior as candidate scores of personality and behavioral flexibility. Two conventional personality traits were measured; “exploration tendency” (a score closely related to boldness, Réale et al. 2007) and “aggressiveness.” In addition, we measured behavioral flexibility as the change in foraging activity with increasing experience. We then determined the dominance status of each individual in a group of 6 fish. Finally, we measured 2 fitness-related traits (survival and growth) and movement in nature. Three questions were addressed:

1. How do individual behavioral traits vary and combine into syndromes?
2. Is variation in these behavioral traits associated with social dominance?
3. To what extent do laboratory-measured variation in individual behavior and social dominance predict fitness-related traits in nature?

## MATERIALS AND METHODS

### Fish sampling and care

During spring 2006, 3 batches of 24 brown trout parr (*S. trutta*, 1 + cohort) were caught by electrofishing in Stenungeån,

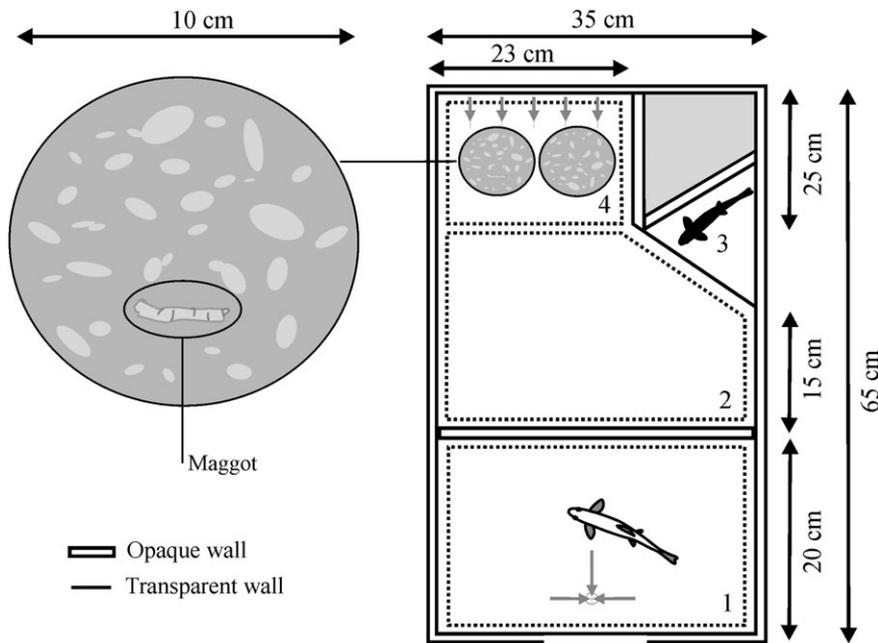
a small coastal stream in western Sweden (lat 58°4'48'' N, long 11° 52'3'' E). Batches were sampled on 24 April, 8 May, and 22 May in 3 different stream sections, each of 60–80 m and separated by 90 and 40 m. Each river section was sampled 3 times and we used a random sample of individuals between 60 and 96 mm (1 + cohort). Each batch of trout was transferred to a holding tank at the department of zoology (University of Gothenburg). Each holding tank (120 l, 40 × 48 × 64 cm) was continuously provided with fresh water (12–14 °C) with a flow rate of 2 l/min and air with an airstone. The photoperiod was adjusted weekly to coincide with the current outdoor light cycle.

During the first week after arrival, fish were allowed to acclimatize to their new environment. Each day, fish were fed one live maggot per individual (pinkies, length 8–10 mm, Fibe AB, Överkalix, Sweden) and 2 g frozen bloodworms (*Chironomidae* spp., commercial fish food supplier) per 24 individuals. On the eighth day after transport, all fish in a batch were anesthetized with 2-phenoxyethanol (0.5 ml/l) and measured for wet weight and length. Each individual was also marked with a colored pearl tag attached to the dorsal fin to enable individual recognition within groups of 6 (Johnsson 1993). The fish were then put back into the holding tank to recover. During this period, fish were fed one maggot per individual and frozen bloodworms (1% of body wet weight) per day. The evening of the 13th day, the first 12 focal individuals (group 1) were transferred to the experimental sequence. No food was provided during the last 24 h before the start of the experiment to ensure a high feeding motivation.

### Individual behavioral traits

Individual behavioral traits were measured over 6 different trials during which each fish was allowed to forage on a cryptic maggot. A previous study using a similar set-up showed that this task is cognitively demanding for brown trout, allowing flexible responses in activity and prey search patterns with increasing experience (Johnsson and Kjällman-Eriksson 2008). Each focal fish was transferred to a flow-through tank where a removable opaque PVC divider separated the start area from the interaction area and the foraging area (Figure 1). The top of the start area was covered with opaque PVC to create a darker refuge area. In the foraging area, we positioned 2 petri dishes, one of which contained a cryptic prey (live maggot, Figure 1). In order to conceal the prey, the petri dishes were covered inside with adhesive folio, matching the color of the prey. In addition, gravel of similar form and color to the prey was spread over the folio. On the bottom of the rest of the aquarium, we spread a 2 cm layer of fine river sand. Next to the petri dishes, we constructed a side compartment in which an “intruder” fish could be placed (intruder compartment). The position of this compartment in relation to the petri dishes (left or right) was pseudorandomized to avoid side effects. The PVC walls of the intruder compartment were opaque toward the petri dishes and transparent toward the rest of the aquarium in order to prevent the intruder fish from seeing the prey, while allowing visual contact between the intruder and the focal fish (Figure 1). Using an air stone in the intruder compartment and 10 small perforations (diameter 3 mm) at the side of its transparent wall, water was allowed to circulate freely between the intruder compartment and the rest of the aquarium. The water outlet in the aquarium was placed so that the focal fish could sense chemical cues from both the intruder and the prey from the start area. We observed the fish through an opening in the black plastic cover at the short end of the tank.

After transfer, the divider was left open allowing the focal fish to explore the experimental aquarium. No intruder fish was



**Figure 1**

Drawing of the experimental set-up for the measurement of individual behavioral traits. Dashed lines indicate the different parts of the tank: 1) start area with water outlet, 2) interaction area, 3) the side compartment with the intruder fish (black), and 4) foraging area with 2 petri dishes for cryptic prey. The opaque PVC divider between the start area and interaction area was removed at the start of each trial. Water level was kept constant at 20 cm, and gray arrows indicate the water current.

present in the interaction compartment at this stage of the experiment. The morning of the following day (day 1), we placed a maggot in one of the petri dishes (randomly chosen). In the evening, fish were gently moved to the start area (without netting), the divider was repositioned, and uneaten prey was removed from the tank. The morning of the second day after transfer, the fish was tested in a series of 6 trials: 4 trials without intruder (day 2 and 3) and 2 trials after addition of the intruder (day 4).

#### *Trials 1–4 without intruder*

Two minutes before the first trial, we positioned a live maggot in a randomly chosen petri dish. The divider was gently lifted to start the trial, and the observer scored the behavior of the focal fish using JWatcher event recording software (Version 1.0, Blumstein and Daniel 2007). To increase the capacity of the behavioral observations, 2 tanks were observed in parallel by 2 observers. The following behaviors were recorded during 20 min:

1) Latency to activity: the time until the fish first started moving. 2) Total active time: the total time spent moving. Fish were considered inactive, if no movement was observed for 5 s. 3) Cryptic prey search time: the time until the fish first touched the prey with the mouth. At the end of each trial, the fish were gently moved back to the start area with the divider closed. A second trial was performed 5 h after the start of the first trial. The whole procedure was then repeated on the third day (trials 3 and 4).

#### *Trials 5–6 with intruder*

The evening after trial 4, we positioned an intruder fish into the intruder compartment to allow acclimatization to its new environment. As the size difference between opponents is known to be an important factor predicting the intensity of agonistic interactions in brown trout (Johnsson et al. 1999), and to simulate the intrusion of a subdominant individual, the length of the intruder fish was standardized to  $86 \pm 2\%$  (median  $\pm$  interquartile range/2) of the length of the focal fish. Trial 5 and 6 took place on the next day (day 4) according to the same procedure as in previous trials. In order to estimate the aggression level, we scored 1) the number of

approaches, 2) number of bites by focal fish directed toward the intruder, and 3) the total time spent in the interaction area (Figure 1).

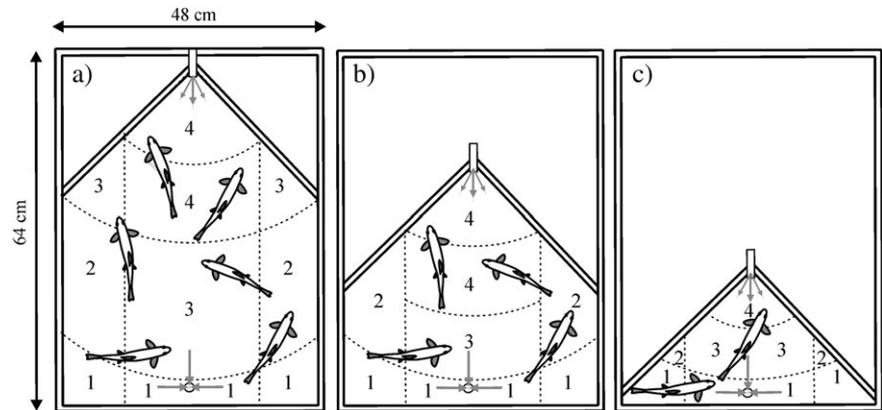
#### **Removal tests to assign dominance status in groups**

The evening after trial 6 of the previous experiment, the 12 experimental fish were pseudorandomly divided into 2 groups of 6 with similar size distribution (in length: degrees of freedom [df] 1 = 11, df2 = 60,  $F = 1.4$ ,  $P = 0.2$ ) and transferred to the next experimental set-up (Figure 2). Both groups of 6 were then left one day (day 5) to acclimatize and fed 6 half maggots. Dominance status was assigned to every individual during the following 3 days.

Dominance status was calculated by a combined index using the following indicators: 1) spatial position in the aquarium, 2) prior access to contested prey items, and 3) aggressive interactions (method modified after Metcalfe et al. 1989; Johnsson 1993). We started the observation in the morning of day 6 by scoring the position of each individual (1–4 points, Figure 2a). After this, half a maggot (to avoid satiation) was entered into the aquarium and the first individual taking the food was given a score of 3 points. During 5 subsequent minutes, we recorded any agonistic behavior and individuals were given an additional point each time they attacked or chased another group member. This procedure was repeated 5 times at 30-min intervals. After 5 trials, we added all scores and the fish receiving the highest score was considered the most dominant. This individual was removed from the tank, and the remaining individuals were left to recover for 2 h. In case the 2 highest ranked individuals differed by less than 5 points, extra observations were performed until the status was resolved. After this, the procedure was repeated until dominance status had been determined for all individuals from 1 to 6 (most dominant), at a pace of 2 trials a day. To reduce any behavioral effects of decreasing density (Sundström et al. 2003), the tank area was reduced after removal of individuals with status 5 (evening day 7) and 3 (evening day 8, see Figure 2b,c). After each reduction of the tank area, fish were allowed to recover for 14 h.

**Figure 2**

(a) Schematic representation of the set-up used for determination of dominance status of individuals in a group of 6. The corners of one short side were shielded by 2 opaque panels and all other sides were covered with black plastic to avoid disturbance. Water level was kept at 20 cm, and gray arrows show the water current. Dashed lines delimit areas with specific position scores from 1 to 4. By releasing prey to the water outlet, position scores correspond with areas of higher value. After removal of the individuals with rank 5 and 3, the experimental area was reduced as indicated in (b) and (c).



### Performance in the wild

After scoring individual behavior and dominance status, experimental fish were returned to the holding tanks and allowed to recover until the next day, when each individual was anesthetized, marked with a passive integrated transponder tag and measured for wet weight and fork length to enable measurement of individual growth after release. At this occasion, we also removed the color tags. All except one individual recovered well from handling (99%). After this, fish were kept in the laboratory holding tanks until release and fed bloodworms (2% of body wet weight per day) in order to ensure good physical condition prior to release. The remaining 12 individuals from each batch (group 2) underwent the same experimental procedure 5 days later and were thus transferred to the cryptic prey set-up on the 17th day after capture. Four weeks after capture and transport to the laboratory, each batch of 24 fish was then transported back to the stream and released in the middle of the river section where they were initially caught. Batch 1 was released at 22 May 2006, batch 2 at 5 June 2006, and batch 3 at 19 June 2006. The mean length of the fish in the 3 batches differed at release (one-way analysis of variance [ANOVA];  $df = 2$ ,  $F = 8.7$ ,  $P < 0.001$ ; mean  $\pm$  standard error [SE]: first batch =  $71 \pm 2$  mm, second batch =  $77 \pm 2$  mm, third batch =  $82 \pm 2$  mm). The distance between the release locations of batch 1 and 2 measured 160 m and between batch 2 and three 110 m.

On the 20 and 21 September 2006, we sampled the whole experimental stream section using electrofishing, starting 130 m downstream the release location of batch 1 and ending 130 m upstream release location of batch 3. To ensure a high recapture rate, we performed 3 consecutive electric fishing bouts. We recorded the identity, recapture location ( $\pm 10$  m), wet weight, and fork length of each recaptured tagged individual.

### Statistical analysis

We used Friedman ANOVA by ranks to test for changes in prey search time across the 6 foraging trials. Separate Wilcoxon signed rank tests were performed post hoc to test for differences between specific pairs of trials.

Principal component analysis (PCA) was used to summarize the variation of 2 different behavioral trait categories (Table 1): foraging activity (an individual's foraging activity during trials 1 to 4) and aggressiveness (agonistic behavior against the in-

truder during trials 5 and 6). Each PCA resulted in one main principal component (PC) with eigenvalue greater than one (Kaiser-Guttman criterion), further referred to as PC foraging activity and PC aggressiveness. Because the use of repeated measures per individual in the same analysis violates assumptions of independent observations, we also ran separate PCA for different trials, resulting in similar components and therefore confirming the validity of our analysis (for a discussion, see also Dingemans et al. 2007). PC foraging activity was transformed with  $-\log_{10}(x + 3)$  to make high values to correspond with high foraging activity and to normalize its distribution (Kolmogorov-Smirnov test;  $Z = 1.09$ ,  $P = 0.19$ ).

We used restricted maximum likelihood linear mixed modeling (LMM, R Development Core Team 2008, library nlme version 3.1-89) to: 1) analyze within and between individual sources of variation in the extracted PC scores (Table 2a), 2) measure and account for fixed effects that could bias the behavioral measures (Table 2b), 3) estimate individual phenotypic values for significant random effects (also best linear unbiased predictors, BLUPs, Henderson 1975). The following

**Table 1**  
Results of PCA on individual behavioral traits

Principal components	PC
PC foraging activity	
Behavior	
Latency to activity (s)	0.86
Total time active (s)	-0.86
Prey search time (s)	0.62
Eigenvalue	1.87
Percentage of total variance	62.41
PC aggressiveness	
Behavior	
Latency to first attack (s)	-0.84
Number of attacks	0.81
Total time near intruder (s)	0.69
Eigenvalue	1.84
Percentage of total variance	61.22

Loadings, eigenvalues, and percentage of the total variance were calculated separately for behaviors describing foraging activity and aggressiveness. PC foraging activity was calculated for 72 individuals and 288 observations, PC Aggressiveness for 72 individuals and 144 observations.

Table 2

(a) Log-likelihood tests between LMMs differing in random effect structure. (b) Estimates of the fixed effects in a LMM containing only the significant random effects

			PC foraging activity			PC aggressiveness				
(a) Random effects										
Model	Ind	Ind × trial	Loglik. <sub>k</sub>	LRT	Chisq <sub>df</sub>	P (%var)	Loglik. <sub>k</sub>	LRT	Chisq <sub>df</sub>	P (%var)
1			-49.39 <sub>11</sub>				-201.84 <sub>12</sub>			
2	<b>x</b>		16.41 <sub>12</sub>	131.61 <sub>1</sub>		<b>&lt;0.0001</b> <sub>(76)</sub>	-183.65 <sub>13</sub>	36.38 <sub>1</sub>		<b>&lt;0.0001</b> <sub>(87)</sub>
3	<b>x</b>	<b>x</b>	21.03 <sub>14</sub>	9.23 <sub>2</sub>		<b>&lt;0.01</b> <sub>(5)</sub>	-183.41 <sub>15</sub>	0.48 <sub>2</sub>		0.7854 <sub>(1)</sub>
(b) Fixed effects										
			β ± SE	F <sub>df1,df2</sub>	P		β ± SE	F <sub>df1,df2</sub>	P	
Intercept			0.31 ± 0.09	241.23 <sub>1,214</sub>	<b>&lt;0.0001</b>		1.28 ± 3.58	0.00 <sub>1,70</sub>	1	
Trial			0.05 ± 0.01	24.09 <sub>1,214</sub>	<b>&lt;0.0001</b>		-0.10 ± 0.50	0.36 <sub>1,70</sub>	0.55	
Batch				0.26 <sub>2,64</sub>	0.77			1.31 <sub>2,63</sub>	0.28	
Group within batch				0.50 <sub>3,64</sub>	0.68			0.35 <sub>3,63</sub>	0.79	
Observer				0.18 <sub>1,64</sub>	0.67			1.94 <sub>1,63</sub>	0.17	
Side of IC				0.05 <sub>1,64</sub>	0.83			0.04 <sub>1,63</sub>	0.84	
Time of day			-0.05 ± 0.10	0.31 <sub>1,214</sub>	0.58		0.22 ± 2.62	0.03 <sub>1,70</sub>	0.87	
Length ratio intruder							-0.98 ± 4.02	0.05 <sub>1,63</sub>	0.83	

Random effect models differed in their random effect structure and were tested against each other (1 vs 2 and 2 vs 3), whereas the full fixed effect structure was kept constant. Random effects are indicated by *x* and noted in bold for the random effect that corresponds with the log-likelihood test on the same line. Variance estimates of the random effects are restricted maximum likelihood estimates of the total variance in PC foraging activity and PC aggressiveness extracted from model 3 excluding all fixed effects (Kontiaainen et al. 2009). Using more standard repeatability measures (Lessels and Boag 1987), differences among individuals account for 51.15% ( $F_{71,216} = 5.19, P < 0.001$ ) of the variation in PC foraging activity and 63.13% ( $F_{71,72} = 4.43, P < 0.001$ ) of variation in PC aggressiveness. PC, principal component. LRT, log-likelihood ratio test. Ind, individual ID. Ind × trial, trial within individual. %var, percentage of total variance. Side of IC, side of the interaction compartment.

fixed effects were added to the initial model: trial number (continuous), batch (3-factor categorical), group (2-factor categorical, nested within batch), observer (2-factor categorical), side of the interaction compartment (2-factor categorical), time of day (continuous, expressed as a value between 0 and 1), length ratio between intruder fish and focal fish (only for PC aggressiveness, continuous). Individual ID was added as a random effect to the model and trial number as a repeated measure within individual ID, thereby allowing for the possibility that individuals differ in their behavioral response to experience (random slope/regression model, Dingemanse et al. 2010). Following methods outlined by Zuur et al. (2009), we used likelihood ratio tests between models differing in random effects, but containing the full fixed effects structure, to test for significance of the random effects. Once random effect structure was determined, fixed effects were tested using Wald statistics. To control whether overparameterization caused fixed effects to be nonsignificant, we also repeated each model to test for each fixed effect separately, leading to similar results. BLUPs were derived from the model containing only significant fixed and random effects. This procedure provided for each individual 2 BLUPs for PC foraging activity. The first, exploration tendency, estimates the activity level in a novel environment (random effect “individual,” Table 2a) and the second, flexibility, the individual change in activity from trial 1–4 (random effect “individual × trial,” Table 2a). Flexibility therefore describes the extent to which individuals adjust their foraging activity patterns when gaining experience with the novel foraging environment. The “individual × trial” random effect not being significant for PC aggressiveness, only one BLUP was extracted for this variable, further referred to as aggressiveness and describing the individual level of aggressiveness toward the intruder fish.

Associations between BLUPs and length were analyzed with Spearman ranked correlation. Effects of initial length, exploration tendency, flexibility, and aggressiveness (independent covariates) on dominance rank were analyzed using ordinal regression (SPSS 15.0, PLUM procedure).

Effects of initial length, exploration tendency, flexibility, and aggressiveness (independent covariates) and batch (3-level

random factor) on recapture rate were analyzed using a binary logistic regression model (SPSS 15.0).

Effects of initial weight, exploration tendency, flexibility, and aggressiveness (independent covariates) and batch (random factor) on absolute growth in length were analyzed using analysis of covariance (ANCOVA, SPSS 15.0). The same model was used to test for effects of exploration tendency, flexibility, and aggressiveness on absolute movement in the stream (in meter, transformed with  $y = \log(x + 1)$ ). Both models were also run using dominance status (fixed factor) instead of aggressiveness, but these results are not presented because neither dominance nor aggressiveness affected absolute growth or movement. For all ANCOVA models, we checked variance inflation factors (VIFs) to ensure that the assumption of independence of variables was met. No variable had a VIF greater than 2, affirming that collinearity was not affecting these results (Quinn and Keough 2002). Repeating all models containing many covariates with single covariates confirmed this conclusion. Residual plots were investigated for deviations to validate the final model, and we calculated Cook’s distance to detect any values exerting extreme influence on the model fit. On the basis of the latter, we removed one value from the analysis for effects of behavior on absolute growth (Cook’s distance = 0.44). To check the robustness of the PCA and LMM analyses, we also performed separate analyses of the individual behavioral traits, which yielded qualitatively similar results (see Supplementary Material).

## RESULTS

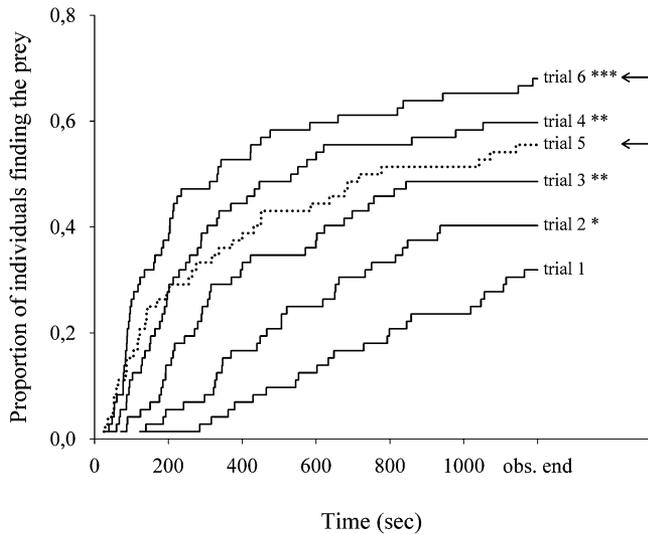
### Individual behavioral traits

#### Foraging success across trials

Fish reduced their prey search time over the course of the 6 trials (Friedman ANOVA by ranks;  $N = 72, df = 5, \chi^2 = 112.8, P < 0.0001$ ). Prey search time decreased for each trial, except for the first encounter with the intruder fish (trial 5, Figure 3).

#### Size effects on behavioral traits

Aggressiveness of the focal fish was not correlated with its size relative to the intruder fish (Table 2b). However, in absolute



**Figure 3**

Time-event graph for the prey search time of all individuals for each of 6 trials. Each line represents for a trial the proportion of individuals finding the prey in function of the total observation time. Arrows indicate trials where an intruder fish was present. To improve contrast between crossing curves, behavior during trial 5 is represented by a dotted line. Stars show significance level of the pairwise comparison of prey search time with the previous trial (Wilcoxon signed rank test; \* $P < 0.05$ , \*\* $P < 0.01$ , and \*\*\* $P < 0.001$ ); obs. end, observation end.

terms smaller focal fish were more aggressive (Table 3). No other effects of size on individual behavioral traits were observed (all  $P > 0.3$ ).

#### Behavioral syndromes

Two pairs of behavioral traits were found to be correlated: slow explorers were less aggressive and showed more flexible behavior (Table 3). Aggressiveness was not associated with behavioral flexibility.

#### Dominance status

Large individuals were more likely to become dominant (ordinal regression;  $N = 72$ , Wald = 17.07,  $P < 0.001$ ), whereas none of the BLUPs for behavior correlated with dominance status (ordinal regression;  $N = 72$ , all  $P > 0.2$ ).

#### Performance in the wild

##### Recapture rate

In total, 48 of 71 (68%) released individuals were recaptured. Recapture rate was not affected by fish size nor by any of the

**Table 3**

#### Correlation matrix for behavioral traits and fish length

		Exploration	Flexibility	Aggressiveness
Length (mm)	$\rho$	-0.15	0.10	-0.37
	$P$	0.215	0.392	<b>0.001</b>
Exploration	$\rho$		-0.58	0.40
	$P$		<b>&lt;0.0001</b>	<b>&lt;0.001</b>
Flexibility	$\rho$			-0.04
	$P$			0.718

$N = 72$  for all tests, and  $P$  values are shown in bold if significant after sequential-Bonferroni adjustment of error rates (Rice 1989).

**Table 4**

#### Association between predictor variables and absolute growth in length in nature

Dependent factor	Effects	df	$F$	$P$
Absolute growth (mm/day)	Batch	2,40	17.77	<0.0001
	Weight (g)	1,40	2.95	0.09
	Exploration	1,40	8.54	<0.01
	Flexibility	1,40	0.0001	0.99
	Aggressiveness	1,40	2.10	0.16

behavioral traits (binary logistic regression;  $P > 0.2$  in all cases).

#### Growth

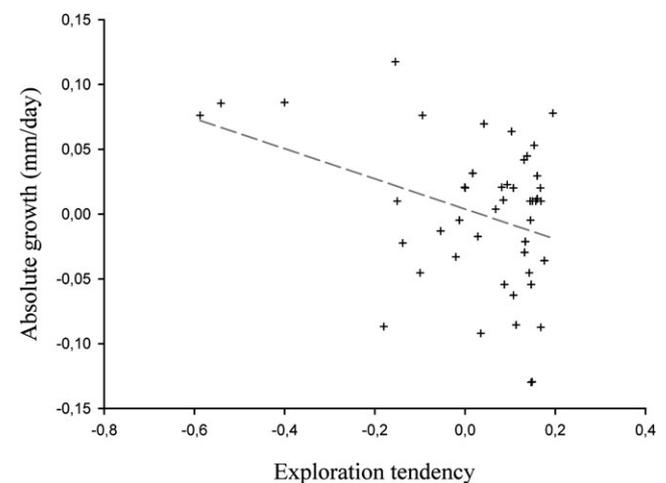
Absolute growth in the wild was negatively correlated with exploration tendency, that is, more cautious individuals grew faster in the wild (Table 4). Batch also had a significant effect, likely reflecting different growth conditions for the 3 batches in the field. Growth was not influenced by any of the other independent variables. Using the residuals of absolute growth to correct for batch effects illustrates the negative relation between exploration tendency and growth rate in the wild (Figure 4).

#### Movement

In total, 69% of the recaptured individuals were caught less than 30 m away from their release point. None of the behavioral traits had any effect on absolute movement (ANCOVA,  $N = 48$ , all  $P > 0.2$ ).

## DISCUSSION

In summary, we found support for behavioral syndromes in brown trout parr with slow exploring individuals being less aggressive and showing more flexible behavior than fast explorers. Aggressiveness scored in the laboratory was a poor predictor of dominance status, and neither of these traits had any effect on growth in the wild. However, slow exploring individuals grew faster under wild conditions. Below, we further explore the 3 main questions addresses in this study.



**Figure 4**

The relation between absolute growth (mm/day) in the wild and exploration tendency. Absolute growth was adjusted for batch (residuals). Exploration tendency was negatively correlated with growth rate ( $P < 0.01$ , see Table 4).

### How do individual behavioral traits vary and combine into syndromes?

In the present study, individual fish differed considerably in exploration tendency, behavioral flexibility, and aggressive behavior. Considering the strong selection on early life stages of brown trout where generally less than 10% of the brown trout fry survive their first year (Elliott 1993), the existence of such broad variation is remarkable, suggesting that a wide range of behavioral strategies can be successful in nature (Andersson 1994; Houston and McNamara 1999). Differences in exploration tendency and aggressiveness were consistent over trials, and repeatability measures were within the range of observed in other species (Table 2, Bell et al. 2009). Further studies will have to confirm whether these personality traits remain stable also over longer periods in the field, as previously demonstrated in other fish species (see e.g., Wilson et al. 1994).

Although the relative size of the focal trout and intruder was standardized, focal fish differed considerably in the intensity of agonistic behavior directed toward intruders where smaller fish were more aggressive (Table 3). Perhaps aggression toward the (even smaller) intruder reflects general motivation in smaller energy-stressed individuals (Lima and Dill 1990), whereas larger individuals are less energy-stressed and therefore less aggressive when alone because they can benefit from their higher resource-holding potential in the group situation (de Laet 1985; Johnsson and Kjällman-Eriksson 2008).

Foraging activity increased with experience (Table 2b, trial effect), which likely reflects cognitive processes such as habituation to a novel environment and learning (Dill 1983; Warburton 2003). The reduction in search time for cryptic prey over trials (Figure 3) illustrates that learning did occur, which is consistent with previous work (Johnsson and Kjällman-Eriksson 2008). However, the appearance of the intruder fish during trial 5 temporarily interrupted the learning process (Figure 3). This suggests that the intruder divided the attention between the focal fish and prey search, which temporarily impaired its prey search efficiency (Dukas 2002). This is not surprising considering the strong territorial behavior normally exhibited by brown trout parr (Johnsson and Forser 2002). Not all individuals adjusted their foraging activity in the same manner and individual variation in behavioral flexibility accounted for about 5% of the total variation in foraging activity (Table 2a, ind  $\times$  trial effect). This estimate corresponds with previous measures of behavioral flexibility (e.g., Nussey et al. 2007; Kontiainen et al. 2009).

We found indications of behavioral syndromes where fast explorers were more aggressive than less explorative conspecifics (Table 3), which is consistent with previous studies in other species showing positive relations between boldness, exploration tendency, and aggression (Huntingford 1976; Réale et al. 2007). More explorative individuals also showed less behavioral flexibility (Table 3), which is in agreement with results from studies on stress coping styles in other species, where aggressive and bold (proactive) individuals tend to build routines, whereas shy and unaggressive (reactive) individuals adjust their behavior more readily to changes in their environment (Koolhaas et al. 1999). Alternatively, however, this negative correlation may follow from the notion that slow exploring fish had more scope for increasing their activity patterns.

### Is variation in these behavioral traits associated with social dominance?

In a variety of taxa, behavioral strategies as well as body size influence social status (Huntingford and Turner 1987). In the present study, length was the only significant predictor of social status, which is consistent with previous studies

indicating the importance of size as an indicator of resource-holding potential (Bradbury and Vehrencamp 1998). Aggressive behavior toward a standard-sized smaller intruder was a poor predictor of dominance status, which suggests that trout modified their aggressive strategy to the social setting they encountered (Krause and Ruxton 2002). Moreover, in contrast to a previous study on brown trout fry (Sundström et al. 2004), we found no correlation between exploration and social status. Other studies have yielded variable associations between bold behavior and social status (Reinhardt 1999; Dingemanse and de Goede 2004) suggesting that this association is highly context dependent.

### Do variation in individual behavior and social dominance predict fitness in nature?

In the present study, most behavioral traits measured in the laboratory did not correlate with fitness-associated measures in the wild (i.e., survival and growth). In addition, social status was not associated with performance in the wild. Indeed, previous studies have challenged the generality of social dominance effects on growth in nature (Martin-Smith and Armstrong 2002; Harwood et al. 2003; Höjesjö et al. 2004). Only variation in exploration tendency affected performance in the wild, where slow explorers grew faster than fast explorers.

Assuming that exploration tendency is stable in nature, and likewise reflects natural foraging activity, energy-saving behavior rather than high foraging activity may account for the observed differences in growth (Careau et al. 2008). Energy-saving behavior is common in several animal taxa, for example, in birds where golden-wing sunbirds avoid rich patches of nectar flowers if the cost of defending them becomes too high (Gill and Wolf 1975). In contrast to the laboratory, trout in the wild are often subjected to strong and variable flow conditions imposing hydrodynamic costs (Fausch 1984). Under such conditions, energy saving low activity levels may be beneficial. Interestingly, more active hatchery trout have been observed to feed less and make less use of energy efficient hydrodynamic positions than wild trout in a natural stream (Bachman 1984). Because a large proportion of the natural prey in trout streams drift with the current, a sit-and-wait strategy linked with high accuracy once the prey is attacked may be favored (De Billy and Usseglio-Polatera 2002). It should be noted that our field experiments were conducted during a period when prey availability generally is high in trout streams (Sandlund 1987). It is possible that risk-prone behavior is more critical for growth when food supplies become limited (Pitcher et al. 1988; Vehanen 2003).

It has recently been suggested that behavioral syndromes can be explained by their association with consistent individual differences in growth rate (Stamps 2007; Biro and Stamps 2008). This view, considering growth rate a cause rather than a consequence of behavior, is compelling. Theory suggests that individuals with very different growth rates can achieve similar fitness through different growth–mortality trade-offs (Stamps 2007). Any behavior (or group of behaviors) that affects an individual's growth–mortality trade-off is therefore expected to show similar individual consistence as the growth rate itself. Central to this argument is the assumption that risk-prone behavior leads to high access to resources and fast growth (or reproductive output, see Biro and Stamps 2008). However, this need not always be the case (Adriaenssens and Johnsson 2009). Braithwaite and Salvanes (2005), for instance, found that hatchery cod with lower responsiveness toward novel stimuli grew faster. Also in our study, the most risky behavior (exploration tendency) caused the slowest growth and therefore contradicts this assumption.

Positive associations between risk-prone personality traits and growth are commonly reported in captive or domesticated animals (Biro and Stamps 2008) including brown trout (Lahti et al. 2001), possibly because domestic conditions are often associated with directional selection regimes favoring rapid growth under relaxed predation risk (Johnsson 1993). In contrast, only few studies have considered association of personality traits with growth rate under natural conditions (Biro and Stamps 2008). These studies suggest that correlations between personality traits and access to resources are more dynamical and often change with environmental conditions (Adriaenssens and Johnsson 2009). Our results are likely the first to report a negative correlation between risk-prone behavior and growth rate in the wild. However, in great tits (*P. major*) and red squirrels (*T. hudsonicus*), the growth of offspring from fast exploring mothers is slower (Both et al. 2005) or occasionally slower (Boon et al. 2007) when compared with slow exploring mothers.

Fluctuations in predation risk (Réale and Festa-Bianchet 2003) and food availability (Dingemanse et al. 2004; Boon et al. 2007) have been put forward as important factors capable of shaping both the direction and intensity of the association between personality and growth. Previous attempts to correlate RNA levels (an indicator of instantaneous growth, Buckley 1984) and behavior in brown trout indicate that bold behavior and growth can either show positive (Johnsson et al. 1996) or no correlation (Sundström et al. 2004). From these variable associations, it may be speculated that fluctuating selection pressures may often disrupt fixed associations between personality traits and individual growth rate. The results of the present study further support this view.

Finally, our results add to the emerging view that fitness interpretations of behavioral traits from laboratory results are extremely difficult and should be made with great caution. Further field experiments are necessary to better understand the selective pressures maintaining personality traits and their variation in natural populations.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

## FUNDING

Swedish Research Council for Agricultural Research and Spatial Planning to J.I.J.; Helge Ax:son Johnsons Stiftelse to B.A.

We thank Marie Karlsson for help in behavioral observations, Jason Pienaar for productive discussions about statistics, and Linus Andersson, Dan Andersson, Torgny Bohlin, Sofia Brockmark, Rasmus Kaspersson, Frida Laursen, and Johan Höjesjö for valuable help in fieldwork. We further thank 2 anonymous referees for their helpful comments on the manuscript. The experiments were approved by the Ethical Committee for Animal Research in Göteborg (License 132/2005) and comply with current laws in Sweden.

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