**Shyer fish are superior swimmers in** **Siberian sturgeon** **(*****Acipenser baerii*)**

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**Abstract**

Differences in individual personality are common amongst animals, which can play an ecological and evolutionary role given links to fitness. Personality affects animal life processes and outputs (e.g., behavior, life history, growth, survival, reproduction), and has become a common theme in animal behavioral ecology research. In the present study, we used Siberian Sturgeon to explore how personality traits of boldness and shyness are related to swimming performance, post exercise recovery and phenotypic morphology. Firstly, our results indicated that the Siberian sturgeon juveniles of shyness were better swimmers, validating evolutionary biology trade-off theory. The critical swimming speed (Ucrit) of the shy groups was higher than that of the bold groups. Secondly, the shy groups were more resilient after exercise fatigue. The swimming fatigue recovery ability, the glucose and lactic acid concentration recovery ability of shy groups were greater than that of bold groups. Thirdly, the shy groups were more streamlined. Compared with bold groups, shy groups had smaller caudate stalk lengths, caudate stalk heights, superior caudal lobes, and inferior caudal lobes. These research results further enrich the theoretical viewpoints of fish behavior biology, more importantly, which provided a good example for studying the relationship between sturgeon’s “personality” and swimming performance.

**Keywords:** individual differences, Siberian sturgeon (*Acipenser baerii*), swimming performance, trade-off, morphology, physiology

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**Introduction**

Animal personality has been broadly defined as interindividual differences in behavior that remain consistent over time and/or contexts [1-6]. At present, research on animal personality has covered diverse taxa including mammals, birds, reptiles, amphibians, fish, arthropods and mollusks [7]. Personality affects animal life processes and fitness, and has become the basis for much research in behavioral ecology [4]. One of the most commonly focused on dimensions of personality is the shyness-boldness continuum. The terms shy and bold refer to the propensity of an individual to take risks, especially in novel environments [8]. Shy individuals react to novelty by retreating, reducing activity levels, and becoming more vigilant, whereas bold individuals are more likely to approach novel objects, and increase activity levels and exploratory behavior [8]. In the case of fish, personality influences various behaviors (including feeding, reproduction, migration, etc.) and is related to physiological processes (e.g., metabolism, immunity), cognitive abilities, morphology, and thus the growth, survival [9].

The study of swimming performance in fish species has a long history, which can be classified as steady swimming or unsteady swimming [10]. The trade-off between the two primary swimming modes, steady and unsteady swimming, is presumed to exist in fish species employing relatively coupled locomotor systems (i.e. the same morphological structures are used for propulsion during both steady and unsteady swimming) [10-11]. One trade-off that is thought to be of general evolutionary importance in fish [12-16]. From an ecological and evolutionary perspective, a trade-off can occur when an increase in fitness due to a change in one trait is opposed by a decrease in fitness due to a concomitant change in another trait [17-19]. For example, northern pike (*Esox lucius*) has much higher swimming velocities during acceleration tests, but poor endurance swimmer [20]. Fitness trade-offs is an ecological mechanism that produce and maintain individual behavioral differences within a population [21]. Personality may be one of the reasons for differences in individual swimming performance within a population. Shy zebrafish (*Danio rerio*) often adopt a strategy of avoiding predators (‘flight’), and exhibit higher steady-swimming performance and thus greater energetic efficiency during routine activities. In contrast, bold zebrafish usually adopt a defensive strategy against predators (‘fight’), showing higher fast-start swimming performance, and achieving greater access to food resources and higher foraging efficiency, meanwhile the risk of predation is higher [21]. The cost-benefit trade-offs associated with energy expenditure associated with personality differences may be one of the most important ecological mechanisms for the generation and coexistence of different swimming performance in fish [22].

Large variations in swimming performance exist among fishes, and morphology are considered to be the main determinants of this diversity of swimming performance [10]. Morphological characteristics associated with swimming can affect the performance of critical activities such as foraging, preator evasion and migration [23]. Morphology differences in body and fin shape is thought to be strong selective pressures acting upon swimming phenotypes [10, 24]. For instance, Australian smelt (*Retropinna semoni*)from river populations tended to have dorso-ventrally deeper bodies and larger heads compared to reservoir conspecifics, with a narrower, fusiform body shape and smaller head [25]. Morphological variation associated with different personality types may also be an important manifestation of variation in fish swimming performance. Studies on zebrafish across numerous generations have found that bold, exploratory, and risk-taking individuals tend to have a more slender body and larger caudal regions, with high fast-start swimming performance and low stable swimming performance, which can improve survival rates in predatory encounters [26-27]. In some cases, certain personalities will only result in improved swimming performance when combined with a specific morphological characteristic [28]. The association between the morphology and swimming performance of fish with different personality traits requires further research.

Physiological variation associated with different personality types may also be an important manifestation of variation in fish swimming performance [29-31]. The metabolic rate of risk-taking carp (*Cyprinus carpio*) is significantly higher than that of risk-avoiding individuals [32]. Moreover, cortisol receptor gene expression, plasma glucose and lactate levels are significantly lower in risk-taking carp than that of risk-avoiding conspecifics [32]. Bold mulloway (*Argyosomus japonicus*) exhibit lower cortisol levels than shy individuals [33]. During the process of uniformly accelerated swimming to fatigue of White bream (*Parabramis pekinensis*), plasma glucose concentration decreased while lactic acid concentration increased [34]. Yet, these studies tend to focus on a single relationship between personality and physiology or swimming performance. Research on how fitness regulates the relationship between physiological performance and swimming performance of fish with different personalities is particularly lacking.

Siberian sturgeon (*Acipenser baerii*), belonging to the class Osteichthyes*,* Actinopterygii, Chondrostei, Acipenseriformes, is the earliest typical trans-estuarine fish group. The species achieves large body size and has a long-life span, and has extremely important scientific value in the study of evolutionary biology [35]. Here, we tested some theoretical concepts in evolutionary biology, 1) Are there personality differences between individuals of Siberian sturgeon? 2) What are the effects of personality differences on swimming performance? 3) What are the effects of personality differences on morphology and physiological performance, which in turn correlates with swimming performance. Findings from this work will further enrich the theoretical knowledge pertaining to sturgeon evolutionary biology, and may help inform conservation efforts for endangered sturgeon species in artificial propagation programs.

**Materials and Methods**

**Source of fish and rearing condition**

One hundred juvenile Siberian sturgeon (mean total length ± SD =15.48 ± 1.80 cm & mean body weight ± SD = 13.13 ± 3.82 g) were collected from Wanming Fishery hatchery farm in Jingmen City, Hubei Province, China and reared in a recirculating aquaculture system at the laboratory of Institute of Hydrobiology, Chinese Academy of Sciences. Water temperature was maintained at 23.0 ± 0.5°C , dissolved oxygen was greater than 6 mg/L and pH was maintained at 7~8, with a 12h:12h light: dark regime. The Siberian sturgeons were fed commercial food twice per day at 8:00 am and 6:00 pm. Healthy fish were randomly selected for experimentation with food withheld for 48h before each experiment.

**Experimental overview**

To control for acclimatization effects, experiments started a month after laboratory housing. We started with the personality test and subjected fish to a classic “boldness” assay[21]. We then assigned individuals to boldness group and shyness group and returned them to recirculating aquaculture system. After 2 rest days we conducted the swimming performance test, a total of 34 bold individuals and 25 shy individuals were tested. Once the swimming performance test was completed, the individual was anesthetized by MS-222 (0.033g/L) and blood was sampled for physiological status analysis. Body weight was measured and pictures of the body were taken (Nikon D810) for morphology analysis.

**Personality test**

A dark/light maze that was divided by a baffle into one shaded (“dark”) arms (5020cm) with a lid on top and one exposed (“light”) arms (5020cm) was used to assess “boldness” (Figure 1). Black cloth around the maze minimized external visual disturbance. Behavior of test fish was recorded with a web camera (BASLER, acA1920-155uc, made in Germany, 25 frames/s) placed about 1.5 m above the maze. For each personality experiment, fish were selected randomly and transferred into a black container (10L) positioned adjacent to the test device. The container was filled with water with the same properties as that of the recirculating aquaculture system. Fish were gently transferred into the shaded arms with the baffle “closed”. After a two minute acclimation period, the baffle was removed and exploratory behavior of the tested fish was recorded with camera. A total of eight minutes were recorded, and after which individual were returned to a separate glass holding tank for further experiments.

Time spent in the dark arms was taken as an indication of “boldness”. Bold individuals were defined as individuals that spent more than four minutes in the exposed arms as per [36-37], and vice versa. However, if fish still had not emerged after eight minutes, the trial was terminated and the individual was allocated a ceiling value of 480s [36-37]. In addition, the animal behavior analysis system (Noldus, Ethovision XT10.0, The Netherlands) was also used to analyze the cumulative exploration time of experimental fish in the exposed arms. The water within the maze was replaced completely between individuals for each experiment. Each individual was repeatedly tested no more than three times, with each retest occurring three days apart to assess short-term repeatability. The fish with same results in two continuous tests was defined as bold individual or shy individual，Otherwise , the experimental fish will be discarded and the selection will be made again.

**Swimming performance test**

We conducted the swimming performance test following the personality test. A self-manufactured swimming tunnel combined with web camera (fixed 1.5m above the swimming device) was used to assess swimming performance (Figure 2). The LS300-type portable flow rate measuring instrument was used to calibrate the flow rate and a linear relationship was established between the flow rate (Y) and the adjustment frequency (X): Y= 0.2517X + 0.6231, R=0.9975 (Figure 3).

Stepped velocity tests were carried out to measure the critical swimming speed of each fish (Ucrit) [38]. The test fish was measured for body length and introduced to the tunnel to acclimate at 0.5BL/s for 2h. Then the water velocity was increased by increments of 1 BL/s every 20min until the fish became fatigued [39-40]. Fatigue was defined as the point at which the fish could no longer swim away from the steel wire mesh positioned downstream of the swimming area (> 20s) [41]. The water velocity and swimming fatigue time (Endurance: defined as the time it took for the fish to stop swimming and fall back to the downstream wire mesh) were recorded. The flow speed was then decreased to 0.5BL/s for a 60 min recovery test, and the recovery time was defined as the time the fish to remove itself from the steel mesh and begin swimming once again. Then a second stepped velocity test was undertaken (the test method was the same as the first time). In each test, the water in the tunnel was the same as that of the recirculating aquaculture system described above. The water was kept aerated when no fish were tested. Videos were playback by Quick Time Player in 0.5 times the speed for the tail beat frequency analysis.

Ucrit were calculated according to equation (1) [42]:

Ucrit = U + ΔU × t/Δt (1)

Where U (cm/s) is the highest velocity at which fish swam for the full-time interval, (cm/s) is the speed step, t (min) is the time to fatigue during the last velocity step and Δt (min) is the time step (20min). The body cross-sectional area of the test fish in this study did not exceed 10% of the cross-sectional area of the swimming area, minimizing the need for a Ucrit correction [43-44].

The recovery ratio (R) of Ucrit (cm/s) was a measure of a fish’s ability to recover from fatigue. A lower R value indicates incomplete recovery and a larger effect of fatigue on subsequent swimming performance. The value of R was calculated using equation (2) [45]:

R=Ucrit2/Ucrit1 × 100% (2)

Where Ucrit1 and Ucrit2 indicated the Ucrit of first stepped velocity test and second stepped velocity test, respectively.

One minute per five minutes videos was selected for swimming states analysis and the average value for each flow velocity gradient in test was calculated. The swimming states of fish were classified into four types according to swimming speed: countercurrent forward: V=M+N, countercurrent stationary: V=M, Float downstream: V=M-N, countercurrent backward: V=N-M. The proportion of each swimming states (P) was also calculated [46]. The value of P (%) was calculated using equation (3):

P =t1/T (3)

Where V is the actual swimming speed, M is the flow velocity, and N is the instantaneous swimming speed of the experimental fish measured by the Ethovision XT10.0. t1 is the duration of a certain swimming state (s), and T is the total observation time (s).

The tail beat frequency (TBF) is the complete tail-beating process of the experimental fish while swimming [47]. Every five minutes a 20s period of video was selected from the whole video to calculate TBF. For each velocity, the value of TBF (times/s) was calculated using equation (4)：

TBF=TBT/t(4)

TBT is the total number of the tail beats of each fish during the period of observation, t is the total time of observation.

**Physiological status test**

After the swimming performance test was completed, the fish was anesthetized by MS-222 (33mg/L) and blood was sampled. Body weight was measured and pictures of the body were taken (Nikon D810) for morphology analysis. The fish was then returned to a holding tank (70×50×20cm) for recovery. Blood was sampled three times at 0h, 3h and 24h, respectively, to understand the recovery pattern of these blood physiology parameters following swimming. In addition, the blood of eight untreated fishes were sampled and analyzed as a control group. The blood samples were stored in a refrigerator (4°C) for 2 hours prior to centrifugation (4000r/min, 20min) while the centrifugal supernatant was stored separately at -20°C. The sample of supernatant was bathed in 4°C water to prevent sample distortion before being tested. Physiological indicators were measured using kits developed by the Nanjing Jiancheng Institute of Biological Engineering and a 721 UV spectrophotometer [48-49]. Glucose and lactic acid and total protein were analyzed to characterize energy consumption in this study, which were determined by glucose oxidase method, colorimetric method and biuret method.

**Morphological characteristics measurement**

Morphological characteristics were analyzed by TPS series software (<http://life.bio.sunysb.edu/morph>). Twenty-one landmark points were selected to obtain the corresponding x, y coordinate values (2D) for geometric morphometry by tpsDig2 (Figure4) [50]. The validity of the landmark points was tested by tpsSmall. Procrustes analysis was used to superimpose the landmark points of all samples by tpsRelw, and the landmark points of each sample were translated, centered, rotated and zoomed. The centroid distance and mean shape were calculated, then, partial warp and relative warp principal component analyses (RWA) were performed. Lastly, the relative warp scores (RW) were used for subsequent analysis [51-52]. The relative warp (RW) was mapped on the thin plate spline to visualize the results [53], while a grid deformation map of all samples was constructed using tpsRegr to analyze and compare morphological differences.

**Data analysis**

T-tests were used to compare the initial differences in body length and weight between bold and shy groups. Two-way repeated measures ANOVA in a general linear model (GLM) was used to assess for differences in swimming performance and physiological indicators between different personality types (shy and bold) over time. The independent variables included personality (two levels: "bold" and "shy") and test (two levels of test: the first and the second stepped velocity test , which formed 4 treatment groups; physiological test at three levels: 0h, 3h, 24h, a total of 6 treatment groups). The dependent variables were swimming performance which including critical swimming speed, fatigue time, fatigue recovery time, and physiological index. For each treatment group, all response variables were evaluated for normality and equal variance using the Shapiro Wilkins normality test as well as density plots.If the data was not normally distributed, it was converted logarithmically. Before assessing whether there was an interaction between personality and testing time, it was necessary to evaluate whether the interaction conforms to Mauchly’s Test of Sphericity. When the conditions of the spherical hypothesis were violated (*p* < 0.05), an epsilon(ε) correction was required, and for epsilon(ε) < 0.75, the Greenhouse-Geisser method was used for correction, while for epsilon(ε) > 0.75, the Huynh-Feldt method was used. When the condition of the spherical hypothesis was satisfied, the covariance matrix of the dependent variable for interaction term personality\*time was equal (*p* > 0.05). Then, we analyzed whether the effect of the interaction on the dependent variables was statistically significant. If the interactions were significant, differences in the swimming performance and physiological index concentrations between the bold and shy groups were compared at different time levels to test the separate effects of the treatment group, and to examine the effect of time alone by comparing differences in time factors between the two personality groups. When only two groups were compared, there was no need to test the spherical hypothesis. Otherwise, the main effects of personality and time were analyzed. If the main effect of a factor with more than two intra-level groups was significant, a pairwise comparison was required. In addition, a one-way analysis of variance (ANOVA) was used to compare differences in the physiological index

concentrations at different time levels between the bold and shy groups and the control group. Differences in the time ratio of swimming state and the tail beat frequency across personality groups were tested by t-test. Hotelling T2 method of multivariate analysis of variance (MANOVA) in a general linear model (GLM) was used to examine and compare differences in relative distortion scores of fish with either personality group. All data analysis and plots were performed in R Studio Version 1.3.1, and significance was considered at an α level of 0.05.

**Results**

**Personality identification**

Consistent interindividual variation in ﬁsh’s tendency to explore the exposed arms were founded. According to the proportion of the cumulative time spent exploring the bright area, 59 individuals could be clearly identified to a personality group, which included 34 bold individuals and 25 shy individuals.

**Swimming performance of different personalities of the Siberian sturgeon**

There were no differences in body length and weight between bold and shy groups. For the swimming performance experiment, the interaction of personality and time had a significant effect on Ucrit (*p* < 0.001). The single effects of personality indicated that the Ucrit of shy groups was significantly higher than that of bold groups (*p*<0.05). The Ucrit of the shy groups increased significantly in the second time test (*p<0.05*), while that of the bold groups decreased (Table 1; Figure 5A, 5B). In addition, the recovery rate of the shy groups (R=104%) was higher than (*p* > 0.05) for the bold groups (R=95%). The interaction between personality and time had no significant effect on the fatigue recovery time of test fish (F1,22=1.59, *p* > 0.05), and the main effects of personality and time had no significant effect on the fatigue recovery time of test fish (*p* > 0.05) (Table 1; Figure 5 C).

The proportion of time of swimming states and tail beat frequency of fish under different flow velocities indicated that bold groups stay in a state of countercurrent forward swimming for a longer period than shy groups (*p* < 0.05), but spend less time in countercurrent stationary and float downstream swimming states than shy groups (*p* < 0.05) (Table 2; Figure 6A). Moreover, the tail beat frequency of fish in the shy group was significantly higher than that of fish in the bold group as the flow velocity increased (*p* < 0.05) (Table 2; Figure 6B).

**Physiological characteristics of different personalities of the Siberian sturgeon**

The personality and time interaction had a statistically significant effect on plasma glucose and lactate concentration (*p* < 0.05). The separate effect of personality at each time level showed that the glucose and lactate concentrations of shy groups was higher than that of bold groups (*p* < 0.05). The separate effect of time showed that the concentrations of plasma glucose and lactate acid in the bold and shy groups changed significantly over time (*p* < 0.05). The results of one-way analysis of variance revealed that at the 24th hour of recovery, the plasma glucose concentration of the shy groups was significantly higher than that of the control group (*p* < 0.05), indicating that the plasma glucose concentration of the shy groups rose faster than that of the bold groups. At the beginning of the recovery (i.e., at0h) the plasma lactate concentration of fish in the shy group was significantly higher than the control groups (*p* < 0.05); at 24h, there was no significant difference compared to control group, indicating that the plasma lactate recovery ability of shy groups was greater than that of bold groups (Table 3; Figure 7).

For total protein concentrations in plasma, the interaction between personality and time was not statistically significant (F1.186, 10.677=1.390, *p* > 0.05). The main effect of personality on total protein concentration was statistically significant, with the mean total protein concentration in the shy group being higher than that of the bold group (F1, 9=6.376, *p* < 0.05). For the main effect of time, the influence of time on total protein concentration was statistically significant (F2, 18=61.861, *p* < 0.001). The results of one-way analysis of variance showed that at 0h, the total protein concentration of the bold group and the shy group was significantly higher than that of the control group (*p* < 0.05); at 24h, there was no significant difference between the total protein concentration of the two groups and the control group. Overall, the total protein concentration of fish declined over time after the swimming performance test, and it was always higher in the shy group than that of the bold group (Table 3; Figure 7).

**The effect of personality on morphological characteristics of the Siberian sturgeon**

In the geometric analysis based on landmark points, the regression coefficients were all greater than 0.99, emphasizing the validity of the landmark points selected. The relative warp principal component analysis extracted a total of 24 principal components, of which the eigenvalues of the first three principal components were 0.331, 0.123, and 0.108, and the total contribution rate was 66.89%, 9.22%, and 7.20%. A total of 83.31% of the intraspecific morphological differences were explained (Table 4). The contribution rate of 21 landmark points in the relative distortion principal component analysis showed that landmark points 12 (deepest part of the caudal fin) and 13 (lower lobe terminal caudal fin) have the largest contribution rate, followed by landmark points 9 (base end of dorsal fin), 10 (dorsal origin of caudal fin), 14 (ventral origin of caudal fin), 18 (origin of pectoral fin), and 19 (lower head end). The total contribution rate of these seven traits was 86.12%. There were significant differences in the caudal fin, caudal stalk, pectoral fin, and head of fishes with different personalities. The Hotelling T2 test showed that the bold and shy groups had significant differences in the former three relative distortions (F3,21=0.914，*p* < 0.05), and that the two personalities of sturgeons had significant differences in RW1 (*p* < 0.05). When the first relative warp was mapped on the thin plate spline, we could visualize its shape (Figure 8). The caudate stalk length, upper caudal lobe and lower caudal lobe of the bold groups were significantly larger than those of the shy groups, while the head height, snout thickness, snout length, body height, and body length of the bold groups were significantly smaller than those of the shy groups.

**Discussion**

Our research showed that there were indeed individuals with different personalities in the Siberian sturgeon population. Individuals with different personalities have not only evolved a series of behavioral differences, but also divergences in physiological performance and morphology. First, we found that shy groups had a significantly higher Ucrit compared to bold groups. Other studies have shown that personality can affect the swimming performance of fish. For instance, in Trinidadian killifish (*Rivulus hartii*), individuals from high-predation sites were faster sprinters but had reduced Ucrit [54]. Shy wild-type zebrafish (*Danio rerio*) were slower in movement and exhibited higher stable swimming performance, while bold fish were more agile and exhibited higher quick-start swimming performance [21]. Fish with different personalities have evolved different swimming strategies depending on their prey and habitat, often at the expense of another form of locomotion [10-11]. This phenomenon is manifested as a trade-off between stable swimming performance (aerobic swimming) and unstable swimming performance (anaerobic swimming), and its ecological mechanism reflects the trade-off between energy gain and cost [15-16,10]. In addition, we also found that the proportion of time that bold groups swam countercurrent forward during the experiment was higher than that of shy groups, while the proportion of time that they were countercurrent stationery and ‘float downstream’ was lower than that of shy groups. This may be related to the fact that bold animals are highly exploratory and aggressive, tend to engage in active avoidance, or cope with stressful stimuli through a “fight or flight” response. Conversely, shy animals typically undertake a passive “freeze and hide” response [55]. The higher tail beat frequency of the shy group with higher flow rates may be related to swimming fatigue in the bold group before reaching the Ucrit of the shy group.

Our research revealed that the morphology of fish differed based on their personality type (shy vs. bold). Shy groups had smaller caudate stalk lengths, caudate stalk heights, superior caudal lobes, and inferior caudal lobes compared with bold groups, while the head height, body height, snout thickness, snout length, and body length were larger in bold fish. Other studies have shown that strong selective pressure affects the morphology of fish with different personalities, and that morphology further affects swimming performance. Western mosquito fish (*Gambusia affinis*) from high predation risk areas have smaller heads and larger tails, and have a stronger ability to start swimming quickly compared to those from low predation risk areas that have larger heads, smaller tails, and more streamlined, stable swimming [56]. It has long been suggested that the divergences in swimming performance occurred, at least partially, via morphological change, as morphology has a significant impact on swimming transport costs [57-58, 26]. Changes in body shape would affect fish hydrodynamics, and ultimately drag coefficients and Ucrit [59-60]. Morphological variations which are poorly suited to produce maximum thrust and minimum drag in GH-transgenic *C. carpio* may be responsible for their lower swimming performance in comparison with non-transgenic controls [61]. The morphology of the fins of juvenile Atlantic salmon (*Salmon salar*) living in slow- and fast-flowing environments differs significantly [62]. In this study, we believe that the larger head and smaller caudal of shy groups made the overall body shape more streamlined, which may minimize recoil energy loss and enhance stable swimming performance [10].

In addition to morphological performance, we also found that the physiological performance of fish with different personalities were different. The ability to recover following swimming fatigue was greater in shy vs. bold groups following the two swimming performance tests. With respect to physiology, the blood glucose concentration of shy fish increased faster than that of bold groups, and the ability to recover from elevated blood lactate levels scavenging was greater in shy fish. Further, their total protein concentrations were always higher than that of bold fish. These findings suggest that personality affects the physiological performance of fish, which in turn affects the swimming performance of fish. Physiological specialization is considered to be one of the main determinants of diversity in locomotor capacities [63]. Prolonged exercise training on the swimming performance of juvenile common carp (*Cyprinus carpio*) revealed that trained fish exhibited higher lactate clearance and significantly increased aerobic swimming performance [64]. Studies have shown that strenuous exercise was found to lead to accumulations of total protein in blood serum, and the increased levels of total protein resulted primarily from lactate accumulation due to anaerobic metabolism in white muscle tissue [65]. Previous studies have shown that physiological traits represent different adaptive strategies to respond to environmental challenges [66]. Different degrees of physiological resilience may be influenced mainly by genetics, environment, and the interaction between genetic and environmental factors [67-68]. In this study, individual differences were measured in the absence of social interaction and with equal and predominantly constant environmental conditions, suggesting that the stronger physiological resilience of shy individuals may be influenced primarily by a genetic basis. In addition, we believe that due to the sufficient energy accumulation caused by the passive “freeze and hide” response of shy groups, and high-level energy reserves could be prioritized for physiological recovery [69]. Previous studies have shown that individual differences in both personality type and energy utilization efficiency affect individual fitness [70-71]. For instance, it is possible that bolder katydid spend more time gathering information about all the available options but owing to the limited time and attention this leads to a lower biomass consumed (i.e. lower foraging efficiency) when compared to shy katydids [72]. We speculate that the bold groups in this study may have spent more time gathering information about potential food choices within the environment, and resulting less time for food [72]. This condition allowed shy groups to benefit by having a higher food intake, maximizing their growth [72]. In addition, because proactive individuals are usually aggressive, dominant, and bold, they are more likely to engage in energetically costly behavior, which leads to higher daily energy expenditure (DEE) and resting standard metabolism [22]. Therefore, it was possible that because the metabolic intensity of bold groups was higher than that of shy groups, the physiological indicators of bold groups were always lower than those of shy groups in the process of fatigue recovery [32].

**Conclusion**

In the present study, different personality types affected the swimming performance of Siberian sturgeon. In general, shy fish had higher Ucrit than bold fish but had poorer fast-start swimming performance. Morphology and physiology also differed across personality types, which may have contributed to the observed differences in swimming performance. Shy sturgeon had relatively large heads and relatively small caudals and had more stream-lined body shapes, which may help to minimize recoil energy loss and enhance stable swimming performance. Bold fish with deeper caudals and smaller heads may be able to generate stronger propulsion, enhancing their ability to start fast. Regarding feeding, bold fish tend to be more exploratory, aggressive and dominant, while shy groups tend to adopt more flexible avoidance strategies when facing pressure, thus showing higher energy utilization efficiency in daily life [62], which would make shy fish have better swimming endurance and physiological recovery ability than bold groups to varying degrees. Our research results further validate the theoretical viewpoints pertaining to the energetic trade-offs associated with an animal’s life-history strategy. A lower Ucrit and slower physiological recovery rate may place bold groups at a disadvantage when competing with shy wild-type groups in their natural habitat, though further research is needed to assess this hypothesis. Our results also provide further knowledge on the links between personality and swimming performance in sturgeon, and theoretical support for improving the conservation of sturgeon. For example, sturgeon could be selectively cultivated with different risk coping styles, so that they not only evolve a range of behavioral differences, but also differences in morphological performance and physiological performance, and selectively release sturgeon with different personality traits for the actual conditions of the natural environment. Future research could investigate other aspects of personality and how these relate to physiology, morphology, and swimming performance in sturgeon.

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**Table 1.** Summary statistics for swimming performance parameters and the results of general linear models (GLM) examining variation in swimming performance parameters between bold and shy Siberian sturgeon.

**Table 2.** Changes in the proportion of time spent in swimming state with different personalities and the tail beat frequency.

**Table 3.** Blood of plasma glucose, lactic acid and total protein levels (Mean±SD) in different personalities test fish at each test stage, and the results of general linear models (GLM) examining variation in different physiological indicators between bold and shy test Siberian sturgeon.

**Table 4**. Eigenvalues and contribution rates of the first 5 principal components of relative warps scores of different morphological features of the test Siberian sturgeon.

**Figure 1**. Experimental apparatus for testing fish personality. The device was divided into 3 parts: A is a cuboid dark area (length×width×height = 50cm×21cm×15cm), equipped with a black opaque lid (E) and an opaque baffle (D); B is a hexagon lit area (side length = 21cm); C is a lit area with the same shape as A.

**Figure 2**. Experimental apparatus for testing swimming performance. A is the rectifier; B is the wire mesh; C is the propeller; D is the swimming test area (50cm×10cm×10cm); The frequency converter controls the motor, and the motor controls the three-blade propeller to create water flow, and the water circulates in the oval swimming tank, and the direction of the blue arrow is the direction of the water flow.

**Figure 3.** The relationship between frequency and velocity.

Control the speed of water flow by adjusting the frequency of the inverter of the device of swimming performance test.

**Figure 4.** The 21 landmarks used for examination of lateral body shape (boldness depicted). 1. Snout tip; 2. Upper snout end; 3. Upper head end; 4. Dorsal origin; 5-6. Dorsal rhomboid primitive spikes; 7. Origin of dorsal fin base; 8. Highest point of dorsal fin; 9. Base end of dorsal fin; 10. Dorsal origin of caudal fin; 11. Upper lobe terminal of caudal fin; 12. Deepest part of the caudal fin; 13. Lower lobe terminal caudal fin; 14. Ventral origin of caudal fin; 15. Origin of anal fin; 16. Origin of pelvic fin; 17. End of pectoral fin; 18. Origin of pectoral fin; 19. Lower head end; 20. Base of operculum; 21. Lower snout end.

**Figure 5**. Swimming performance of different personalities. Blue and red represented bold sturgeon and shy sturgeon respectively; FS and SS represented the first and second swimming performance test respectively. A was the critical swimming speed, B was the swimming fatigue time (endurance), and C was the fatigue recovery time.

**Figure 6**. Changes in the proportion of time spent in swimming state and the tail beat frequency with different personalities. Blue, red and yellow represented 1BL/s flow rate, 2BL/s flow rate and 3BL/s flow rate, respectively. Figure A showed the time proportion of swimming state of sturgeon with two personalities at different flow velocity. Figure B showed the tail beat frequency of two personalities at different flow velocity.

**Figure 7.** Physiological changes in different personalities. 0h, 3h and 24h are the fatigue recovery time of the test Siberian sturgeon; Glu, LD, TP are the concentration of glucose, lactic acid and total protein in the blood respectively.

**Figure** **8.** Grid deformation and variation visualization of morphological features of bold (a) and shy (b) test Siberian sturgeon .