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Individuality in Fish Behavior: Ecology and Comparative Psychology

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Abstract—This work is a brief review of a series of studies of the phenotypic organization and ecological significance of individual differences in fish behavior. The following species were studied: the guppy *Poecilia retuculata*, the lion-headed cichlid *Steatocranus cassuarius*, and the convict cichlid *Archocentrus nigrofasciatum*. We developed methods for the analysis of individual differences in fish behavior and studied their structure, development, and ecological and evolutionary significance.

Individual differences in animal behavior are attracting more and more interest of researchers (Slater, 1981; Dunbar, 1982; Caro and Bateson, 1986; Clark and Ehlinger, 1987; Mendl and Deag, 1995). Such an interest is especially pronounced in the behavior of fishes (Magurran, 1993; Wilson *et al.*, 1994; Coleman and Wilson, 1998). Many studies have revealed substantial differences between conspecifics in feeding, defensive, sexual, and other behaviors (see reviews by Ringler, 1983; Magurran, 1993). Significant individual differences were found even in the behavior of fish in schools (Radakov, 1972; Helfman, 1984; Magurran, 1993; Pitcher and Parrish, 1993), which was for a long time considered as the most homogenous social structure (Shaw, 1970; Radakov, 1972). Even the classical example of many textbooks, the stereotypic response of male three-spined sticklebacks (*Gasterosteus aculeatus*) to red stimuli, is very variable in different individuals. It differs so significantly (very pronounced in some individuals and completely absent in others), that the classical concept of innate releasing mechanisms can be questioned (Rowland, 1982; Baerends, 1985; Bolyard and Rowland, 1996).

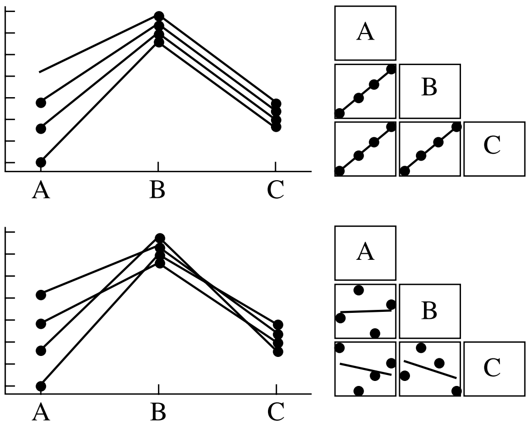
Individual differences are important primarily because they are the basic material for evolution (Darwin, 1859). The basic ecological and adaptive mechanisms maintaining individual differences in behavior within a single population are currently known. They primarily include the frequency-dependent selection (Wilson *et al.*, 1994; Wilson, 1998).

Nonetheless, most studies of individual differences in the behavior of fish and other animals until now involved only the adaptive value of isolated behavioral elements and tactics. Motivational mechanisms of individual differences remain almost unclear. Also absent is a unitary comparative approach, including the study of the phenotypic structure of individuality, its motivational determinants, as well as ecological and evolutionary significance.

We conducted a series of studies (Budaev, 1997a,b; Budaev and Zhuikov, 1998; Budaev *et al.*, 1999a, 1999b; Zworykin *et al.*, 2000) aimed at the analysis of the phenotypic organization and ecological significance of individual differences in fish behavior. These studies included development of methods for classification and analysis of individuality, analysis of its structure in fishes of several species, analysis of the development of behavioral individuality in the ontogeny, and ecological and evolutionary significance. The most important results of these studies are reviewed in this paper.

Individuality: How to Measure It?

In the study of any differences between species, populations and individuals, the basic unit of analysis is character (Yablokov and Larina, 1985; Mina, 1986; Yablokov, 1987, 1988). The concept of character includes any trait which can vary between species, populations, or individuals (Michener and Sokal, 1957; Langlet, 1971; Mina, 1986). In the study of morphological and physiological variation, characters are not very difficult to define and measure. However, in behavioral studies, this is often not an easy task. The behavior of each individual depends on both its motivational state in a particular time and the immediate environmental stimuli. Even under controlled experimental conditions it is almost impossible to create a completely identical environment for all individuals. They receive and respond to somewhat different stimuli. It is also impossible to exclude the random variation of behavior, the more so that natural selection can maintain even completely random behavioral tactics (Cooper and Kaplan, 1982; Labas and Krylov, 1983; Kaplan and Cooper, 1984). All this at first glance completely contradicts the



An illustration of behavioral consistency. Connected points depict four individuals; left panel: the overall individual level of a particular behavior in three situations (A, B, C); right panel: between-situation correlations (scatterplots). Low average level and high variability of the behavior is observed in situation A, high average level and low variability of this behavior is observed in situation B, and low average level and low variability in C. However, individual differences may be consistent (upper row) or inconsistent (lower row).

possibility to find stable individual characteristics of the individual.

This problem, the extraction of stable characteristics of individuality from constantly changing overt behavior in response to the environment, is important not only in the study of animal behavior. It first appeared in the beginning of the 20 century in psychology when it became necessary to measure such “immeasurable” phenomena as intellect and personality. This is why psychologists developed a system of methods for the extraction of stable characteristics of personality and factors of intelligence, which could be used also in the study of animal behavior (Harrington, 1988).

Two different aspects of stability are usually distinguished in psychology and psychometrics (Eysenck, 1970; Eysenck and Eysenck, 1985): there is a fundamental distinction between “stability” and “consistency.” When one speaks of stability of a certain behavior, this usually means that this behavior does not change. Consistency of a particular behavioral measure means that it is characterized by high predictability or correlation during repeated measurement (temporal stability or continuity) or across various situations even if the overall average level of this measure changes (Nunnally, 1967; Ozer, 1986). For example, an individual exhibiting a higher level of aggressiveness than other individuals in one situation could also be more aggressive than others in another situation even if the behavior overall differs in these situations (figure). Thus, the behavior may be situation-specific, whereas individual differences are consistent.

The Structure of Individuality in the Guppy

The aim of the first study was the analysis of individuality in the guppy *Poecilia reticulata* (Budaev, 1997a; Budaev and Zhuikov, 1998). In planning the study, we tried to answer the following questions: (1) Are individual differences in this fish consistent over time and across situations? (2) If yes, is it possible to extract basic characteristics of individuality, most determining the differences between individuals? (3) Is this interindividual variation continuous or does it represent some sorts of alternative types, similar to alternative coping strategies found in other animals (Benus *et al.*, 1991; Verbeek *et al.*, 1994)? (4) What are the main motivational mechanisms of consistent characteristics of individuality in the guppy?

For the study, we used feral guppies inhabiting a stream from a sewage station. Each individual was tested in four tests with repeated administrations. The interval between the tests was one month. First, the fish were tested in a large open field, a hexagonal tank with a diameter of 1 m, where we recorded their locomotor activity.

One month after the third testing in the open field test, the guppies were tested in the predator inspection test. It was conducted in an aquarium with three compartments. First, the fish was released into a small compartment, separated by an opaque partition with a door. This was an imitation of a novel environment without foreign orients. After 5 min of testing, we opened the door leading to the second inspection compartment. This compartment was separated by a transparent partition from the third compartment, containing an individual convict cichlid *Archocentrus nigrofasciatum*, which served as a model of a predator. Further, we recorded various behaviors of the tested guppy: movements, freezing at the bottom, hanging in midwater, darts, and active escapes. Also, we recorded the predator inspection behavior, which was defined as approach to the model predator followed by more or less prolonged visual fixation on it (Magurran and Girling, 1986; Magurran and Seghers, 1990).

The test measuring the group tendency was conducted in a two-section aquarium, separated by a transparent partition. One compartment contained a group of four guppy individuals. The mirror test was organized similarly, but instead of the group, a mirror was attached to one wall of the aquarium. In these two tests, we recorded the same behaviors as in the predator inspection test. In addition, in the group tendency test, we also recorded attempts of the tested subjects to “go through” the glass to the conspecific group and, in the mirror test, any interactions with the fish’s own mirror image.

The fish were also tested in a two-way avoidance response in the shuttlebox (Leshcheva and Zhuikov, 1989). The conditioned stimulus was illumination by two lamps; the unconditioned stimulus, mild electric current.

The results of the study revealed significant correlations (Cronbach reliability coefficient $\alpha = 0.74–0.90$, $r = 0.50–0.84$) between most behavioral variables measured during repeated testings in the same tests (even though the average values of certain behavioral measures could change during repeated testings, in tests of exploratory behavior, these changes reflect the effect of habituation). Thus, individual differences in the guppy are highly consistent over a relatively long time.

This consistency allowed to aggregate the repeated measures of each individual, which allowed to reduce the large number of variables and represent the individual differences in the most economical way (Epstein, 1983). Another advantage of this data aggregation procedure is that it has the same effect as increasing the sample size: reduction of random variation and the measurement error (Epstein, 1983), thereby increasing the stability of correlation matrices.

To extract the basic characteristics of individuality reflecting the inherent differences between individuals, we conducted factor analyses of the composite measures obtained after aggregation. Factor analysis of behaviors scored in the exploratory behavior tests (open field and the predator inspection test) revealed two factors. The first factor was associated with activity in the open field, movements in the novel environments and in the presence of the predator model, predator inspection, and (negative correlation) freezing. Therefore, it was interpreted as **Activity–exploration.** The second factor was most correlated with freezing and escape responses, which allows to interpret it as **Fear–avoidance**.

The second factor analysis, in which we included the behaviors recorded in the group tendency test and the mirror test, also resulted in two interpretable factors. The first factor was associated primarily with locomotion, and the second, with the group tendency (tendency to get into the compartment with conspecifics) and interactions with the mirror image. Therefore, the second factor was interpreted as **Group tendency**. Further data analysis indicated that the factor **Activity–exploration** was significantly correlated ($r = 0.60–0.90$) with measures of the group tendency. Thus, the basic characteristics of individuality in the guppy were **Activity–exploration**, also associated with the tendency to contact with conspecifics, and **Fear–avoidance**.

Analysis of discontinuous variation indicated that freezing in the novel environment and the latency to exploration of the novel environment and the model predator had bimodal distributions. This supports the results of other studies (Nechaev *et al.*, Pottinger *et al.*, 1992; van Raaij *et al.*, 1996), also documented active and passive behavioral types within the same species of fish.

Results of experiments on training of fish to avoid electric current in the shuttlebox (Budaev and Zhuikov, 1998) indicated that the characteristics of learning capacity of individual guppies significantly differed. Furthermore, higher individual values on the **Fear–avoidance** scale facilitated the earlier appearance of correct avoidance responses (more fearful individuals required less presentations of the conditioned and unconditioned stimuli until they began correctly responding, $F_{1.19} = 12.56$, $p < 0.01$) and, therefore, faster learning. More fearful guppies were also characterized by a smaller number of trials until the longest series of consecutive avoidances (Cox F test: $F_{10.20} = 2.84$, $p < 0.05$). These results agree with the modern theories of learning, that the motivational state of fear plays an extremely important mediating role in avoidance learning to aversive stimuli (Gray, 1987).

Development of Individuality in the Lion-Headed Cichlid

If, as previous studies showed, fish really have a consistent individual “temperament,” the question arises as to how and when does appears in the ontogeny? This question was addressed in a special study conducted on west-African lion-headed cichlid *Steatocranus cassuarius* (Budaev *et al.*, 1999a).

First, 12 individuals were selected for the experiments. Each fish was tested in three tests, similar to those used in the previous study: in the open field, stranger fish test (the stimulus fish was a large individual of the convict cichlid), and the mirror test. The fish were tested two times, at an age of 4 and 5.5 months. Later, the second group of 14 fish was taken from the same population. This group was also tested in the same tests, first at 12 months and then at 13.5 months. In all tests, we recorded various behavioral units: movements, freezings, inspection of the stranger fish, aggressive behaviors directed at the mirror image, etc.

The results of the study indicate that individual differences were not consistent at an age of 4.0–4.5 months. But consistency increased later, when the lion-headed cichlids reached the age of 12.0–13.5 months (Spearman correlation coefficient $\rho > 0.6$, $p < 0.05$).

Very interesting results were obtained during analysis of relationships between the body size and individuality in the ontogeny. For example, during the first two testings, aggressiveness and the time spent near the strange fish significantly correlated with the body size (Spearman correlation coefficient $\rho = 0.6–0.8$, $p < 0.05$). But at the age of 12 and 13.5 months, the correlation between body size and behavior completely disappeared. Thus, larger body size stimulated higher boldness and aggressiveness in fish at the age of 4–5 months, which was probably mediated by its effects on early social status. However, development of consistent individual characteristics at later stages of the ontogeny and increase of their role reduced the dependence of behavior and the body size. A similar pattern has been documented in other studies (Francis, 1990).

Individuality, Mate Choice, and Parental Behavior in the Convict Cichlid

The studies reviewed above showed that fish of several species have individual temperaments, which completely develops in adults. Therefore, it is very interesting to consider the ecological significance of individuality, especially its role in mate choice and parental care. Separate studies (Budaev *et al.*, 1999b; Zworykin *et al.*, 2000) were devoted to these questions.

We took 80 individuals of the convict cichlid *A. nigrofasciatum*, which were kept in a large tank with potential spawning substrates, where individuals could freely form pairs. The pairs were then transferred to individual aquaria, where they were maintained during the subsequent experiments. We observed the formation of pairs, spawning, and parental behavior of the fish at various stages of offspring development, and measured the offspring ration. One of the most important components of parental care in the convict cichlid is parental food provisioning by stirring up the bottom substrate (Wisenden *et al.*, 1995; Zworykin, 1998; Zworykin and Budaev, 2000). Therefore, we concentrated on this component of parental behavior. In addition, all individuals were tested in a series of tests similar to those in the previous studies: open field, inspection test (we used an individual *Pterophyllum scalare* as the stranger fish), and the mirror test. Various behaviors were recorded in these tests, e.g., movements, freezings, inspection of the strange fish, aggression, etc.

Factor analysis of the measures obtained in the behavioral tests revealed two factors. The first factor was associated with locomotor activity and freezing in the absence of the stranger fish. The second, with locomotor activity and inspection of the stranger fish. Therefore, these factors were called **Activity** and **Activity–exploration**. Because these two factors were correlated, we also extracted the second-order factor **Boldness**. Aggressive behavior correlated negatively with **Boldness** (Spearman correlation coefficient $\rho = -0.32$, $p < 0.05$). Factor analyses, conducted separately for males and females, did not show any structural differences, even though females had, on average, higher values of **Boldness**.

Analysis of pair formation revealed clear assortative mating with respect to the temperament factor **Boldness** in the spawning fish: bolder and more active males tended to form pairs with bolder and more active females (Spearman correlation coefficient $\rho = 0.49$, $p < 0.05$). It is especially important to note that such assortativeness was absent in the pairs which were initially formed, but later broke without spawning (Spearman correlation coefficient $\rho = -0.31$, $p > 0.05$). Results of the analysis of parental behavior pointed to high consistency of individual differences in parental brood provisioning (Cronbach reliability coefficient $\rho = 0.92$). In males, the intensity of parental food provisioning significantly correlated with individuality ($p > 0.05$): less aggressive, more active and exploratory males were characterized by a higher intensity of food provisioning. However, in females, the intensity of parental brood provisioning was not related to individuality. Interestingly, both the frequency of parental brood provisioning and locomotor activity were significantly correlated between males and females within the pair (respectively, Spearman correlation $\rho = 0.59$, $p < 0.05$ and $\rho = 0.88$, $p < 0.05$). In other words, both parents within the pair tended to behave similarly.

As expected, a higher intensity of parental food provisioning during parental care was associated with a higher number of more profitable large larvae of *Chironomidae*, which tended to occupy deeper horizons of the bottom substrate and were not available to the offspring without parental assistance (Spearman correlation coefficient $\rho = 0.79$, $p < 0.001$). This clearly brought about faster growth of the offspring (Spearman correlation coefficient $\rho = 0.90$, $p < 0.001$). However, after termination of the parental care period, when the young fed without parental assistance, the intensity of prior parental brood provisioning did not correlate significantly with the offspring body size (Spearman correlation coefficient $\rho = 0.33$, $p > 0.05$). Even more, a higher intensity of prior parental brood provisioning caused a reduction in the offspring's ability to hunt for small larvae (Spearman correlation coefficient $\rho = -0.59$, $p < 0.05$), which were the basis of their ration. Thus, the fry of parents with a lower level of parental care obtained more individual experience of searching and hunting for small larvae, whereas the offspring of "better" parents, without such experience, became less capable to hunt for the available food organisms.

DISCUSSION

The results of our studies evidenced that individual differences in fish behavior may be very consistent over time and across situations. Furthermore, behavioral individuality could be considered at several levels of abstraction. On the lowest level, we have separate behavioral responses, at the higher, one can extract more general characteristics of individuality. In our studies, the basic individuality characteristics were **Boldness**, i.e., the propensity to take risks in potentially dangerous situations (Wilson *et al.*, 1993, 1994; Wilson, 1998; Budaev, 1997b), and **General activity**, including locomotor activity, exploratory behavior, and tendency to contact conspecifics.

It is especially interesting, that similar characteristics of individuality were found in many groups of vertebrates, including mammals (Budaev, 1997c; Gosling and John, 1999). For example, modern theories

(Eysenck, 1970; Eysenck and Eysenck, 1985; Zuckerman, 1994) posit that the basic characteristics of human personality include **Emotional stability** (emotionality, susceptibility to anxiety, and fear) and **Extraversion** (general activity, susceptibility to exploratory behavior, impulsiveness, and sociability).

Such similarity of individuality structure in various groups of vertebrates could point to common genetic, physiological, motivational, and adaptive mechanisms. Indeed, evolution is a historical process, and it could be expected that certain fundamental behavioral mechanisms may be found in species with a common origin (Darwin, 1872; Severtsov, 1922).

It is known (Watson and Tellegen, 1985; Meyer and Shack, 1989) that the structure of temperament and personality is significantly linked with emotions. But fundamental neurophysiological mechanisms involved in basic emotions are very similar in various mammals (Panksepp, 1982; Simonov, 1981, 1987; Gray, 1987). Furthermore, the functions of the limbic system of the brain involved in emotions in mammals and the forebrain in fish are very similar. For example, effects of lesioning and electric stimulation of the fish forebrain and mammalian limbic system are very comparable (Flood *et al.*, 1976; Nikonorov, 1982). It is quite possible that certain homologous genes are involved in the formation of basic emotions (or emotion-like processes) and individuality in various groups of vertebrates.

Thus, the terms “temperament” and “personality” could be used for the description of animal behavior, even lower vertebrates. Temperament and personality is a system of consistent individual characteristics which are associated with the type of nervous system. The most important characteristics of temperament and personality are consistency over time and across situations (Eysenck, 1970; Buss and Plomin, 1975; Strelau, 1983; Eysenck and Eysenck, 1985; Goldschmidt *et al.*, 1987; Zuckerman, 1994). As we have shown in our studies, individuality in fish satisfies these criteria.

The pattern of the development of temperament traits in the fish ontogeny—increasing consistency with age—agrees with the data obtained for other species. For example, studies on mammals indicated that individual differences are inconsistent early in the ontogeny, but become more consistent with age (MacDonald, 1983; Loughry and Lazari, 1994; *Developmental Behavior Genetics*, 1990). The same tendency is observed in humans (e.g., Plomin, 1986). We expect that this universal tendency is associated with conservative mechanisms of development and integration of behavior control systems (Hogan, 1988; Karmiloff-Smith, 1994).

The significant consistency of temperament and the fact that they could appear in various situations make temperament very important in an ecological sense. For example, our studies revealed assortative mating with respect to the level of boldness in males and females. This evidences that temperament plays an important role in mate choice in fishes. Temperament determines characteristics of parental care, especially such an important element as food provisioning. At the same time, the pattern of parental brood provisioning significantly affects the subsequent life of the offspring. The importance of temperament for fish ecology is also supported by the data, indicating that fish with different temperaments differ in habitat preference, the structure of the ration, characteristics of schooling behavior, etc. (Wilson *et al.*, 1993; Budaev, 1997b).

Thus, temperament could provide an important element for the comparative and integrative approach to the study of behavior, unifying analysis of general phenotypic structure of individuality, possible motivational and physiological mechanisms, and their ecological and evolutionary significance.

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