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Individual Differences in Behavior and Mechanisms of Ecological Differentiation on the Example of Fish

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Abstract—In this paper we present a review of the individual differences in animal behavior as exemplified by fish. A review of the basic ethological approach to their study is given. Terms such as “temperament” are shown to be applicable to the description of stable characteristics of individuality in animals. It should be emphasized that consistency over time and across situations is the main classification characteristic of the temperament trait. We also briefly review genetic and physiological mechanisms of individuality in fish, factors affecting their development in the ontogeny, and the effects of individual experience. Temperament is shown to have significant adaptive value: in many cases natural selection maintains alternative behavioral tactics. We also consider the main quantitative models that account for the coexistence of individuals with different behavioral patterns. Finally, it is demonstrated that patterns of behavioral individuality may significantly affect population dynamics.

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Investigations of individual differences in animal behavior have been conducted, to one or another degree, since the time of Darwin or even earlier (Slater, 1981; Caro and Bateson, 1986; Ehlinger, 1987; Sih et al., 2004a, 2004b; Réale et al., 2007; Budaev and Brown, 2011). Such interest is fully justified, since individual differences, including those in behavioral traits, represent “raw material” for both artificial and natural selection. Intrapopulation variation and alternative strategies of social, reproductive, feeding, migratory, and other patterns of behavior are currently well described in the literature. A recent statistical meta-analysis[1] of the available literature demonstrated that over 10% of the variation of behavioral elements is linked to individuality (Bell et al., 2009).

It is very likely that individual behavioral differences are the most widely studied in fish, which is related to the great biological diversity of these animals that dwell in the most varied aquatic ecosystems. The convenience of keeping fish under controlled laboratory conditions is also important. Numerous investigations revealed considerable differences between the individuals in the most diverse behavioral patterns, including social, feeding, defensive, migratory, sexual, etc. (Ringler, 1983; Magurran, 1993; Budaev and Zworykin, 2002; Pavlov et al., 2007; Budaev and Brown, 2011; Conrad et al., 2011). Considerable individual differences were found in the behavior of fish in a school (Radakov, 1972; Pitcher et al., 1982; Helfman, 1984; Magurran, 1993; Pitcher and Parrish, 1993; Ward et al., 2004; Leblond and Reebs, 2006), which was regarded for a long time as the most homogeneous, equipotential social structure (Radakov, 1972). Even the example of rigidly species specific instinctive behavior—the stereotype response of the male of the three-spined stickleback to a red belly of the same (a classic example for ethology)—in reality strongly differs in separate individuals: it is rather pronounced in some and completely absent in others. According to the opinion of some researchers (Rowland, 1982; Baerends, 1985; Bolyard and Rowland, 1994), this calls into question the classical concept of key stimuli-releasers that turn out to be neither universal, nor highly specific.

In this work we present a review of recent investigations of individual differences in fish behavior, as well as of their adaptive importance and mechanisms of ecological differentiation. As listed above, the phenomena of behavioral individuality as a whole and individual differences in particular is rather wide. It includes both differences in the manifestation of simple unconditioned reactions and individual specific features of complex forms of defensive and social behavior of individuals. In this paper we mainly consider the latter—relatively complex forms of behavior. Because of their considerable flexibility, the study of mechanisms, as well as of the ecological and adaptive importance of individual differences of complex forms of defensive and social behavior, is most difficult for analysis.

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[1] Meta-analysis is a statistical methodology that allows the combination of results of several published investigations for quantitative verification of a definite hypothesis.

APPROACHES TO THE INVESTIGATION OF INDIVIDUAL DIFFERENCES

The concept of *character* (phenotypic or genetic) in a wide sense is the basis of modern biology. A character is a base unit in describing differences between species, populations, and individuals (Yablokov and Larina, 1985; Mina, 1086; Yablokov, 1987). The concept of the character includes any trait that can vary between species, populations, and individuals (Michener and Sokal, 1957; Langlet, 1971; Réale et al., 2007; Mina, 1986). In studying morphological variation, it is rather simple, as a rule, to determine characters; for instance, usually it is not difficult to measure the length or weight of an animal or some of its morphological structures.

In behavioral investigations, the separation of consistent characters that may characterize separate individuals is usually a problem. Animal behavior is actually rather flexible and represents a set of adaptive responses to diverse external and inner stimuli. Even under well-controlled experimental conditions, it is difficult to create a completely identical medium for all individuals. They may differ by preceding experience or motivational state, etc. For instance, predator presence beyond the barrier may cause strong stress in fish having encountered a predator but curiosity (exploratory behavior) in individuals without such experience (Brown and Warburton, 1999). Fish can use different strategies depending on the behavior of other individuals in the group (Davies, 1982; Krebs and Davies, 1993). Finally, one cannot exclude also "...accidental variation uncontrolled and frequently inseparable from behavior measurement" (Jinks and Broadburst, 1974, p. 8). This is all the more important, since natural selection can support "mixed strategies" when animal with a definite probability selects one from the fixed set of strategies (Maynard Smith, 1982) or even completely accidental behavior ("adaptive coin-flipping," Cooper and Kaplan, 1982; Labas and Krylov, 1983). Thus, a separate behavioral indicator measured at some moment in some situation hardly represents a classical character capable of reliably characterizing separate individuals.

There are several general approaches to describing individual differences in behavior using slightly different terminology. Nevertheless, the terminology and conceptual apparatus in the given field are only now being formed. Therefore, the differences between them are rather conventional and in many respects are determined only by an accent on definite types of behavior and the used terminology. For instance, some researchers in studying individual differences of behavior operate mainly by generalized characteristics of individuals (for instance, "boldness"), while others distinguish groups of individuals characterized by similar values of determined phenotypic characteristics (such as "active" and "passive" strategy). Different approaches, however, are united by the fact that the researcher attempts to distinguish in flexible behavior relatively consistent characteristics. A consistency in the characters in such a case can manifest itself *at different moments and in different situations* (Budaev and Zworykin, 2012; Budaev and Brown, 2011).

It is important to note that tolerance has no relation to the stability or invariability of a particular behavioral element. On the contrary, individuals can demonstrate rather consistent individual differences, even in higher-degree, labile forms of behavior. Tolerance of individual differences means *correlations* in behavior. In an ideal case, this means that the ranking of individuals by the degree of manifestation of some form of behavior remains invariable with time in different situations. For instance, most (at the least) aggressive individuals remain such in two situations, even if the general level of aggression in these situations considerably differs (Budaev and Zworykin, 2002; Réale et al., 2007; Budaev and Brown, 2011). It is of interest that the deviation of individual values of the behavior of a separate individual from the line of regression predicted from the presence of behavioral correlation—syndrome deviation—in some cases also turns out to be rather demonstrative (Herczeg and Garamszegi, 2011).

The consistency of individual differences *at different moments* is based on a concept such as *repeatability* of behavior. In the simplest case, repeatability is the coefficient of a correlation between two measurements of the same behavioral character at different moments upon the repeated testing of individuals in the same test. In the general case, repeatability is an intraclass correlation coefficient estimated by methods of correlation or dispersion analysis, as well as on the basis of models of mixed effects (Nakagawa and Schielzeth, 2010). With ideal repeatability, all measurements are a simple linear function, and the corresponding coefficient is equal to unity. Meta-analysis of the repeatability of behavior in different investigations demonstrates (Bell et al., 2009) that its average value is 0.37 and usually increases with decreasing intervals between measurements. For instance, the repeatability of boldness characteristics in cichlid fish *Neolamprologus pulcher* decreases from 0.83 when measurements are performed in one day to 0.19 for measurements separated by an interval of three years (1201 day) (Chervet et al., 2011).

Statistical meta-analysis of the great volume of literature accumulated to date supports the existence of consistent individual differences (Bell et al., 2009; Garamszego et al., 2012). Nevertheless, the size of the effect is not always considerable and can strongly differ in different populations of the same species (Garamszegi et al., 2012). This indicates that the pattern of individual variability can, to one or another degree, reflect an adaptive response to concrete environmental conditions.

Shyness–Boldness

At the dawn of the modern surge of interest in individual differences in behavior, Wilson et al. (Wilson et al., 1993, 1994) suggested the shyness–boldness continuum as a fundamental characteristic of individuality in different species of animals. The authors gave an operational definition of the given continuum as "an individual tendency to avoid or an inclination for risk." Shyness–boldness is frequently used for fish. For instance, the same team of authors (Wilson et al., 1993) used it to describe individual differences of behavior in the common sunfish *Lepomis gibbons*. In this investigation, the shyness–boldness continuum was determined by the inclination either to avoid or approach new objects. A long ruler, as well as a small fixed net, were used as new objects. It turned out that bold individuals characterized by a weakly pronounced avoidance of new objects (as well as of the diver approaching them for observation) were distinguished by a declined tendency for group behavior and were more rapidly acclimatized under laboratory conditions. The location of separate individuals on the shyness–boldness continuum allowed the prediction of specific features of their feeding, a preferable use of particular biotopes, and specific features of parasitofauna. Similar results were obtained by Budaev (1997a) on Black Sea ocellated wrasses *Symphodus ocellatus*. Those ocellated wrasses that behaved most boldly in a new unknown environment (i.e., moved actively, manifesting exploratory behavior) in nature preferred open biotopes and were distinguished by a poorly pronounced tendency toward schooling behavior. Shy individuals—those that were not active in a new environment and instead of exploratory behavior tried to hide themselves—attempted to be in a school and preferred vegetated biotopes.

The concept of shyness–boldness was used in several subsequent investigations of fish. It is most often determined by a test in an open field—a new, unknown environment devoid of the typical fixed markers—and tests based on the presentation of unknown objects of different sizes and shapes, models of predators, or a live predator located beyond a transparent screen. In addition, the time before fish begin to feed in a predator's presence, the time before fish move independently to an unknown section of the aquarium from the "home" section through a small opening in the partition, and the time passed in a potentially dangerous open microbiotope, etc. are often measured to determine boldness. Most investigations reveal a considerable consistency of similar behavioral characteristics, i.e., individuals manifesting high boldness in one test manifest boldness in other tests also (Huntingford, 1976; Brick and Jakobsson, 2002; Ward et al., 2004; Brown et al., 2007; Wilson and Godin, 2009). At the same time, it turned out in some cases (Coleman and Wilson, 1998; Wilson and Stevens, 2005; Dingemanse et al., 2007) that the boldness indices of fish in different situations were not always correlated. In other words, the same individual could be bold in one test but shy in another. Investigation of the shyness—boldness continuum is important, since the behavior of individuals in risky situations usually has an important ecological and adaptive value and is related to a multitude of other forms of behavior representing important mechanisms of ecological differentiation (Wilson, 1998; Cote et al., 2010; Dingemanse and Wolf, 2010).

Strategies of Reacting to Stress

A slightly different approach to the description and analysis of individual differences in animal behavior, including fish, is based on the concept of coping with stress[2]. Within such an approach, the main strategies used by different individuals to cope with a stressful situation are determined. In this case separate groups of individuals characterized by a particular type of response to stress are usually distinguished (Budaev, 1997b; Budaev and Zworykin, 2002; Brelin et al., 2005; Øverli et al., 2007; Budaev and Brown, 2011). In this case two alternative strategies of overcoming stress are more frequently distinguished: proactive and reactive (Benus et al., 1991; Koolhaas et al., 1999; Øverli et al., 2007). Research on mammals and birds (Koolhaas et. al., 1999; Bakshi and Kalin, 2002; Coppens et al., 2010), and, to a lesser degree, on fish (Øverli et al., 2005), demonstrated that alternative strategies of coping are related to a multitude of neuroendocrine differences, as well as metabolism intensity.

The same behavioral tests for studying shyness–boldness are used to study coping: testing on an open field, different novel objects, model predator, etc. are used. Individuals characterized by a proactive response to stress are distinguished by higher activity, boldness, aggressiveness, a tendency toward a more stereotypical response and indifference to small changes in environmental status. For instance, proactive individuals manifest a pronounced exploratory behavior upon the presentation of an unknown object; however, they examine such objects rapidly and superficially. Individuals characterized by a reactive strategy, on the contrary, are more timid and less aggressive. More sensitive to environmental changes, they examine new stimuli slowly but more carefully.

Behavioral Syndromes

Yet another approach to the study of individual differences in behavior is based on the concept of a behavioral syndrome. A syndrome is a set of intercorrelating types and indices of behavior connected with each other within one situation or in different situa-

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[2] Coping in psychology means the general strategy of reacting to stress, including cognitive, emotional, and behavioral components. Psychobiological and psychopharmacological models of coping have been elaborated for rodents and primates.

tions (Sih et al., 2004a, 2004b). A classic example of a syndrome is the correlation between the level of activity, boldness, and aggressiveness in different situations observed in individuals of the three-spined stickleback *Gasterosteus aculcatus* (Tulley and Huntingford, 1988). Sih et al. (2004a) noted several syndromes having, in their opinion, particular importance: those of aggressiveness, activity, boldness, timidity, and reactivity.

The correlation between behavior in different situations, as well as the correlation between different types of behavior, are important, since they can generate adaptive trade-offs when the same character has high benefit and cost. Hence, syndromes can play an important role in behavioral evolution. The correlation between individual behavior in different situations impose limitations on adaptive flexibility and, hence, the possible direction and rate of evolution (Sih et al., 2004a; Dochtermann and Roff, 2010).

For instance, high boldness can be adaptive in a situation in which there is competition for food. However, in the presence of a predator, boldness can turn out to be not adaptive, since it increases an individual's risk of being eaten. Similarly, high aggressiveness increases the competitive ability of an individual when it searches for food; however, such an aggressive individual can also attack a nuptial partner, which also seems disadaptive. The presence of a behavioral syndrome in many cases makes it possible to explain the presence of an obviously disadaptive behavior: though disadaptive in isolation, this type of behavior turns out to be adaptive because of its correlation with other related behavioral forms (Sih et al., 2004a; Budaev and Brown, 2011).

Temperament

Still another trend of research on individual differences in animal behavior, including fish, is based on an extension of the concept of temperament, and even personality, to animals (Budaev, 1997b; Gosling, 1999; Budaev and Zworykin, 2002; Vazire et al., 2007; Uher, 2008). Within this research trend, temperament is determined as "...a complex of individual specific features of an individual primarily related to the type of nervous system determining behavior in different situations" (Budaev, 2000, p. 15). As for personality, it includes temperament characteristics, which area related to social behavior and are determined by the life of individuals in the community. These definitions are operational and do not imply the presence of developed emotions, cognitive capacities, or consciousness, and the nervous system is determined as "a conceptual cognitive system" in the sense of Hebb (Hebb, 1955). Therefore, the terms "temperament" and "personality" can be used to describe the behavior of a wide range of organisms (even, for instance, bacteria), as well as that of artificial agents (e.g., robots) (Budaev and Brown, 2011).

Researchers studying human personality have elaborated concepts, approaches, and methods that make it possible to isolate and analyze stable elements in the highly flexible behavior of *Homo sapiens*. The existence of consistent personality traits is quite obvious at an intuitive level; however, their quantitative study began in psychology beginning from the 20th century (Cattell, 1957). Nevertheless, personality theories based on the analysis of consistent personality traits had also serious critics. For instance, one of the most influential critics of personality theory, Mischel (1973), asserted that there is no stable personality in fact and that human behavior is highly labile and mainly depends on external stimuli (here, Mischel's theory has something in common with classical behaviorism). Nevertheless, the existence of consistent personality traits is no longer doubted (Kaurick et al., 1988). Human behavior is actually very flexible, and personality characteristics do not allow the prediction of each isolated behavioral act; they only describe the tendencies, usual modes of action, and typical behavior of an individual over a long period of time (Fleeson, 2004; Funder, 2009). The same approach—the separation of consistent individual characteristics—can be applied to the study of animal behavior. Within this trend, researchers are mainly interested in revealing the main regularities or base factors—a sort of a general "landscape"—of individual differences in the behavior of animals of different species and groups (Budaev, 1998; Gosling, 2001; Réale et al., 2007; Vazire et al., 2007; Budaev and Brown, 2011; Uher, 2011).

Individuals are usually tested in a set of several tests measuring several indices. Tests are repeated over time to reveal the consistency of individual behavior indices. At the concluding stage, multivariate statistical analysis of a great number of variables is performed, which allows one to reveal the main factors of the temperament of the given species of the highest order (Budaev, 1997b; Budaev, 1998; Budaev and Brown, 2011). Precisely such an approach is also used by psychologists to study human personality—only, instead of behavioral tests, psychological questionnaires and rating scales are used (Cattell, 1973; Vazire et al., 2007; Uher, 2008, 2011). This research trend can be exemplified by the work of Budaev (1997b), who identified in the guppy *Poecilia reticulata* consistent temperament factors, activity and fear, on the basis of behavior of these fish in a set of different test situations.

The study of animal temperament and personality corresponds to the classical paradigm of ethology described in the famous work by N. Tinbergen "On Aims and Methods of Ethology" (Tinbergen, 1963). This work, which formed the basis of modern ethology and the ecology of behavior, begins with the section "Observations and Description," which emphasizes the importance of determining the general picture—a sort of a general landscape—of behavior. The concept of a temperament and personality of animals also follows the ethological tradition of the functional and operational determination of complex forms of behavior expressed by Konrad Lorenz in his Nobel lecture: "When we speak of falling in love, of friendship, personal enmity, or jealousy in these or other animals, we are not guilty of anthropomorphism. These terms refer to functionally determined concepts, just as do the terms legs, wings, eyes, and the names used for other bodily structures that have evolved independently in different phyla or animals" (Lorenz, 1974, p. 233).

Individual Characteristics and Phenotypic Groups

From the discussion listed above, it is seen that the description and analysis of individual differences in behavior can be based on separation of individuals into phenotypic groups (for instance, the coping strategy in a stressful situation is divided into proactive and reactive individuals) or distinguishing individual phenotypic *characters* (for instance, the level of boldness of each individual). In the first case, the researcher separates the whole totality of animals into natural groups or clusters (types of individuality) in correspondence with a definite phenotypic criterion. In the second case, the analysis unit is a behavioral characteristic, and animals are ranked according to the corresponding scale. Although the separation of individuals into phenotypic groups seems more intuitive, we think that the second approach is more general and productive for the study of individual differences in behavior. Actually, the separation of clusters into an obvious or nonobvious form reflects one or several phenotypic characteristics (for instance, groups "large" or "small" differ by the characteristic "body size"). The separation of groups is most natural in those cases when determining the characteristics that have bi- or multimodal distribution or when the researcher deals with discrete strategies (tactics) representing a sequence of actions, decision trees, etc. not described by the usual incessant variables (rank or order scale). If the distribution is unimodal (for instance, approaches normal), the separation of groups inevitably has an arbitrary pattern. In any case, separation as an analysis unit of phenotypic characteristics allows an easy description of groups or types of individuals, while the separation of a group is determined by the presence of natural inhomogeneity/bimodality.

Mechanisms of Individual Differences in Behavior and Temperament

It is reasonable to suppose that correlations between different forms of behavior of individuals in different situations reflect the presence of genetic, physiological, neuroendocrinal, ontogenetic, motivational, adaptive, or evolutionary mechanisms limiting independent variation of behavioral variability. Genetic correlations emerge, for instance (Falconer and MacKay, 1996), as a result of the pleiothropic action of genes (the action of a specific gene on more than one phenotypic trait) or the result of a non-random association of alleles in different loci (linkage disequilibrium). Moreover, the mere existence of a phenotypic correlation between traits frequently indicates (although this is not obligatory) that there may also be agenetic correlation between these characteristics (Cheverud, 1988; Bakker, 1994; Roff, 1995; Dingemanse et al., 2012). Phenotypic correlations between behavioral characteristics forming behavioral syndromes more frequently coincide in direction with genetic ones and, on average, explain up to 75% of the dispersion of the latter (Duchtermann, 2011).

Correlations can be determined also by limitations placed on ontogeny—a limited set of possible ontogenetic states, as a result of ordering in time, or functional limitations, such as limitations on values of magnitudes or of their combinations (Arnold, 1990, 1994). It is also supposed (Gray, 1987; Bakker, 1994; Depue and Collins, 1999; Budaev and Brown, 2011) that a correlation between different forms of the behavior of separate individuals are determined by general physiological, motivating, or psychological factors controlling these forms of behavior. For instance, if a general motivation system controls a set of behavioral elements, these elements should respond to external factors similarly. Moreover, a high (or low) level of activity of the given system in definite individuals should manifest itself in a more (or correspondingly lower) pronounced manifestation of all forms of behavior (in different situations) controlled by the given system.

It is known that the characteristics of human personality (Livesley et al. 1998), dogs (Saetre et al., 2006), and birds (Oers van et al., 2004, 2005), as well as those of other species of animals, have a hereditary component. Temperament characteristics in fish can be also determined genetically, and recent investigations made it possible to obtain approximate estimates of the coefficient of their inheritance (h^2). For instance, Brown et al. (2007) compared the level of boldness in *Brachyrhaphis episcopi*: descendants of fish from two populations with different predation pressures. Fish from s population with a high level of predation were bolder than individuals from population with a low level of predation. Differences between the descendants of fish from the given populations cultivated in the laboratory were of the same ratio as in the parental populations. Wright et al. (2003) found significant differences in boldness levels and tendencies of manifestating team behavior of the zebrafish *Brachydanio rerio*, descendants of fish from four wild populations. In this case the inheritance coefficient level approached 0.4. In contrast, a rather low inheritance coefficient for boldness and aggression, $h^2 < 0.2$, in two populations of three-spined stickleback was found in the work by Bell (2005). This can indicate a strong selection pressure that "washes out" most of the adaptive genetic dispersion. However, it is possible that boldness in these populations of fish is determined mainly by environmental conditions.

Another group of researchers (Dingemanse et al., 2009) tested three-spined sticklebacks from populations with high and low predation pressures. The fish were also subjected to repeated encounters with predators, which also allowed an assessment of the effect of individual experience. As it turned out, the inheritance index of boldness and general activity, as well as the tendency to manifest group behavior, fluctuated from 0.06 to 0.32. It is important to note that the level of inheritance in an overwhelming number of cases was considerably higher in populations sympatric with predators. This corresponds to data showing that behavioral syndrome (correlated boldness, aggressiveness, and activity) is pronounced precisely in those populations with high predation pressure and does not manifest itself to full measure in populations devoid of predators (Dingemanse et al., 2007).

Wright et al. (2006a) investigated quantitative trait loci (QTL) for boldness and the tendency to manifest team behavior in a recombinant population of zebrafish obtained by crossing wild fish with individuals of a laboratory line. The investigation made it possible to distinguish two loci of quantitative traits determining differences between individuals by the level of boldness in chromosomes 9 and 16. This indicates that variations of this temperament characteristic are determined by a relatively small section of the genome of these fish, which more likely includes a multitude of genes. Moreover, the same group of authors (Wright et al., 2006b) revealed epistatic interactions of genes determining the boldness level in zebrafish. This indicates a rather complex pattern of inheritance of the given property of temperament, including the interaction of separate genes. On the whole, the separated pattern nearly corresponds to the inheritance pattern of traits exerting a considerable impact on the components of adaptation.

It is known that temperament characteristics of mammals and birds, particularly those related to boldness, are considerably determined by hormonal mechanisms of the reaction to stress and coping strategies (Koolhaas et al., 1999, 2011). Similar data were obtained also for fish. For instance, individuals of *Brachyrhaphis episcopi* distinguished by great boldness demonstrate a relatively weak hormonal reaction to stress (Brown et al., 2005). A similar relation between boldness and hormonal reactions to stress was found also in other fish species (Øverli et al., 2005; Schjolden et al., 2005; Rauoult et al., 2011). A recent study demonstrated interrelation between a bodily response to stress and coping strategy in the carp *Cyprinus carpio* (Huntingford et al., 2010). Bold individuals were distinguished by a considerably higher metabolic intensity than timid individuals. The level of gene expression of the cortisol receptor and the lactate level in the plasma and glucose of bold fish was lower. A similar interrelation between boldness and the background concentration of blood cortisol was revealed in the mulloway *Argyosomus japonicus*, in which bold individuals had also a considerably lower level of cortisol concentration than timid individuals (Raoult et al., 2011).

Intrapopulation differences in the migratory behavior of the roach *Rutilus rutilus* reflect differences in the concentration levels of substances of the catecholaminergic system. For instance, it was shown in the paper of Pavlov et al. (1998) that individuals with high and low levels of DOPA, dopamine, and cortisol occur in the river; however, fish with intermediate concentration levels of these substances are practically absent. Thus, roach larvae are differentiated during the period of its mass downstream migration into two distinct groups. Juveniles from the group with a decreased content of hormonal substances dwell in the limnoconditions of coastal biotopes and do not participate in downstream migration (resident group). Juveniles of the second group have a higher level of the mentioned hormones. They stay in a boundary site, in the current closer to the channel flow, and perform downstream migration (group of migrants). It is of interest that individuals from the group with a high level of hormones are characterized by an inclination for risk; for instance, they are more likely to enter a new environment (Nechaev et al., 1991). The behavioral differences of fish from the revealed groups are evidently based on different synthesis leels of those hormones that immediately regulate energy processes in the body, primarily catecholamines and corticosteroids (Pavlov et al., 2007). For instance, the placement of residents in the current leads to a disturbance of the rates of anabolic and catabolic processes and the development of stress response. Individuals of the resident group can be in rheoconditions only for a relatively short time (Pavlov et al., 2007).

A group of researchers (Øverli et al., 2005) bred two lines of rainbow trout *Parasalmo* (*Oncorhynchus mykiss* with high and low reactivity to stress. The selection criterion was a high (HR line) or low (LR line) poststress cortisol concentration in plasma. It turned out that these lines considerably differ by their physiological characteristics and behavior in different tests, which indicates differences in their temperament (Øverli et al., 2007). For instance, fish from the HR line were distinguished by the presence of stress-induced anorexia: unlike fish of the LR line, they did not feed during the poststress period (Øverli et al., 2002). Individuals of the LR line were also distinguished by higher boldness and aggressiveness, and they usually occupied dominant positions in the social hierarchy (Pottinger and Carrick, 2001). Experiments on trained fish demonstrated that fish of the LR line were characterized by a considerably longer decay of the conditioned conventional-reflex response to learned stress than fish of the HR line (Moreira et al., 2004). Thus, the line with low reactivity to stress (LR) demonstrated boldness and activity, as well as the low behaviorial flexibility typical for active coping, as was previously shown for mammals (Bonus et al., 1991; Koolhaas et al., 1999; Bolhuis et al., 2005) and birds (Groothuis and Carere, 2005).

The neuroendocrinal differences between HR and LR lines of rainbow trout also include differences in the activity and metabolism profiles of the monoaminergic brain system (Øverli et al., 2001). For instance, the HR line is distinguished by higher levels of the synthesis and metabolism of serotonin, noradrenaline, and dopamine in the poststress period than the LR line. In turn, individuals of the LR line are characterized by an increased level of 5-HIAA (serotonin metabolite) and MHPG (noradrenaline metabolite) in the hypothalamus, as well as a higher level of the background ratio of 5-HIAA/5-HT to telencephalon. On the whole, these patterns considerably coincide with the picture observed in mammals differing in coping strategies (Øverli et al., 2007).

It is known that the limbic system of the brain, including the hippocampus, tensil, hypothalamus, and several other adjoining structures, plays an important role in controlling emotions and personality formation in humans and other mammals (Gray, 1987; Laurin, 2002). Although the brain organization in fish considerably differs from that in mammals, certain sections of the forebrain—the lateral and medial pallium—are regarded as homologs of the limbic system (Flood et al., 1976; Nikonorov, 1982; Wullmann and Mueller, 2004; Yamamoto et al., 2007). In fish these sections control similar behavioral mechanisms and processes, such as, for instance, emotional learning (Nikonorov, 1982; Broglio et al., 2005; Portavella and Vargus, 2005). Nevertheless, what impact is exerted by these structures of the forebrain on individuality remains practically unknown.

Recent investigations of zebrafish indicate the possible involvement of particular structures of the epithalamus, especially of the habenula, in the formation of emotions, individual differences in behavior, and lateral asymmetry in fish. The habenula is one of the main dorsal components conducting intermediate brain routes that connect the limbic sections of the forebrain, as well as the midbrain and posterior brain (Sutherland, 1982; Bianco and Wilson, 2009). It is of interest that it is asymmetrical in fish and some other groups of vertebrates: the left lateral nuclei of the habenula considerably exceed the right in size (Bianco and Wilson, 2009). A spontaneous mutation changing the given asymmetry in zebrafish causes a considerable increase in boldness (Dadda et al., 2010). In addition, the development of a zebrafish embryo in complete darkness at early stages of ontogeny exerts an impact on the asymmetrical development of the light-sensitive habenula nuclei (Budaev and Andrew, 2009a), and—what is most interesting in the given context—considerably affects the development of boldness (Budaev and Andrew, 2009b).

More and more evidence has recently been accumulated that the habenula is among the key sections stimulating the dopaminergic system of the brain, which in turn plays an important role in the formation of anxiety and fear, as well as the personality characteristics related to them (Shepard et al., 2004). This indicates a considerable similarity of the structure of individual differences, temperament, and personality in different species of vertebrates—from fish to humans. In all likelihood, the basic characteristics of temperament and personality reflect a conservative evolution, i.e., limitations on evolution that are due to the effect of homologous physiological and genetic mechanisms.

ONTOGENY AND EFFECT OF INDIVIDUAL EXPERIENCE

Individual temperament characteristics in fish, as in other animals, demonstrate considerable consistency in ontogeny. For instance, in the midas cichlid *Amphilophus citrinellus* (*Cichlosoma citrinellum*), the ranking of individuals by their aggressiveness does not change from the first month of life to the onset of maturity (Francis, 1990). Slightly different results were obtained in a study of the development of boldness and aggressiveness in the African lion-headed cichlid *Steatocranus cassuarius* (Budaev et al., 1999a). While individual characteristics did not manifest themselves in the behavior of immature individuals of the given species, correlations between behavior in different test situations (hence, consistent characteristics of temperament) were revealed after the onset of maturity. In other studies (Budaev and Andrew, 2009b; Conrad and Sih, 2009), consistent individual characteristics, such as boldness, were pronounced already in early ontogeny—in larvae (zebrafish and rainbow trout, respectively). Such an early manifestation of consistent individual differences can be induced by an encounter with a predator and considerably modified by environmental factors, such as light (Budaev and Andrew, 2009a, 2009b).

The resident and migratory groups of roach individuals listed above differing by their hormone levels are formed mainly due to energy factors that act during early ontogeny (Pavlov et al., 2007). Upon the separate incubation of individual eggs, their differentiation does not occur. When eggs are incubated in a group, late embryos differentiate into two groups by the activity level of the dopaminergic system and the activity of metabolic processes related to steroidal hormones. It is of interest that the addition of water in a tank with individually incubated eggs into water from the general clutch also induces hormonal differentiation (Nechaev et al., 2000; Pavlov et al., 2007). Thus, the hormonal and behavioral differentiation of juvenile fish emerges as a result of the impact of metabolites of other individuals in the group, which indicates its important role in the minimization of intraspecies competition (Pavlov et al., 2007).

Individual experience can considerably affect boldness. For instance, in the work of Wilson et al. (1993), differences between bold and shy sunfish were rather noticeable in nature and immediately after placement in aquariums. However, such differences disappeared after prolonged isolation under laboratory conditions. Imitation of a predator's attack increased the boldness of individuals of *Brachyrhaphis episcopi*, descendants of fish from populations with both high and low predation pressures (Brown et al., 2007). Swedish researchers (Hellström and Magnhagen, 2011) compared the boldness levels of individuals of perch *Perca fluviatilis* from two populations with different predation pressures. Descendants of fish from the given populations cultivated in a medium without predators, as turned out, did not differ in boldness. Thus, individual experience can exert an important impact on the formation of boldness, and possibly of other individuality characteristics of fish.

A change in the composition of a group of fish is capable of considerably modifying characteristics of the behavior of shy individuals of perch and, to a lesser degree, of bold individuals of this species (Magnhagen and Staffan, 2004). Shy fish, for instance, became bolder when they were placed in a group of shy fish. Bold fish, after being placed in a group of bold individuals, on the contrary, decreased their boldness. Similar data were obtained by these authors in another investigation (Magnhagen, 2006). In the latter case, the correlation between the time passed by perches in a potentially dangerous medium and their exploration of an unknown medium (which in combination forms the characteristic of boldness) was statistically significant only in the case when the behavior of other members of the group was considered statistically.

The experience of victory and defeat in aggressive interactions, or even the mere observation of the behavior of shy or bold individuals of its own species, can modify boldness levels in rainbow trout (Frost et al., 2007). The sex of the partner in the group also in some cases affects the boldness of an individual. For instance, guppy males manifest more pronounced boldness after an attack by an aerial predator when they are in a group of males rather than females (Piyapong et al., 2009). A similar strong effect of the social environment on the manifestation of boldness and other individuality characteristics can be expected in fish species that pass a considerable part of their life in a group (Brown et al., 2011).

The importance of individual experience and social environment for the support of individual differences in boldness is stressed by the possibility of a spontaneous reversion of the coping strategy in lines of rainbow trout with high and low reactivity to stress. For instance, in one case, after transportation from Great Britain to Norway, fish of the HR line began to demonstrate bolder behavior than fish of the LR line and exhibit social domination. At the same time, differences between the lines' hormonal profiles remained (Raiz-Gomez et al., 2008). This unexpected result indicates that a cardinal change in the environmental conditions (transportation procedure, as well as other conditions of keeping) is capable of modifying even consistent individual differences in behavioral coping strategy.

The learning capacity of the fish itself is subjected to considerable individual differences; these differences can be related to other individuality characteristics, e.g., boldness. For instance, in the works of Lescheva and Zhuikov (1989), differences were revealed in the rate of teaching individuals of the Atlantic salmon *Salmo salar* and the guppy for the task of two-way avoidance in a shuttle box. In these tests, an electrical shock was the unconditioned stimulus, and lamps were switched on as the conditioned stimulus. To avoid the electric shock, the fish had to move to the opposite section of the shuttle box. The tests demonstrated that, while some individuals elaborated a stable reaction of avoiding, others turned out to be incapable of it and rather rapidly passed to a passive-defensive behavior reminiscent of "conditioned helplessness." A third behavior type was characterized by the elaboration of a defensive reaction that, however, turned out to be unstable and was quickly inhibited. Finally, some fish demonstrated rapid learning: consistent conditioned-reflex activity appeared without a preceding period of inconsistent activity. Similar individual differences in learning avoidance were found in other fish species (Zhuikov and Trunov, 1994), which is evidence in favor of the universality of the given phenomenon.

It is of interest that the rate of training guppy individuals in a two-way shuttle box is considerably determined by the level of their similarity (Budaev and Zhuikov, 1998). Less bold individuals are trained more rapidly. This observation agrees with the two-process theory of avoidance learning (Zhuikov et al., 1994; Zhuikov, 1995), which postulates that its general rate is determined by the development rate of a "conditioned fear" reaction and the development of an instrumental reaction (movement of an individual to an opposite section). In all probability, shy individuals are distinguished by a relatively easy elaboration of the reaction of conditioned fear related to an intense locomotory reaction in response to an aversive stimulus, which promotes rapid learning in the given situation (Budaev and Zhukov, 1998).

In learning tasks related to the search for new food, a higher rate is demonstrated by bold individuals manifesting more active exploratory behavior (data on guppy (Dugatkin and Alfieri, 2003). Moreover, it was shown (Mesquita, 2011) that bold carp individuals are characterized by a more chaotic strategy of learning. It is important to note that the behavior of fish individuals in different learning tasks (for instance, learning, inhibition of conditioned reaction, repeated learning) related to foraging behavior can demonstrate considerable consistency (data on the common sunfish *L. macrochirus*, Colgan et al., 1991).

Individual characteristics can themselves exert a considerable impact on specific features of social interaction between individuals, which creates an additional level of social structure complexity. For instance, the social networks formed by guppy individuals in a group (Croft et al., 2004) are characterized by a considerable degree of nonrandomness and assortativeness; shyer individuals have many more connections (Croft et al., 2005). These data considerably coincide with results obtained for three-spined sticklebacks (Pike et al., 2008). Thus, shyer fish can perform the role of a kind of "key individuals" on which the structure of the entire social network and maintenance of its integrity depends to a maximum degree (Krause et al., 2010).

Under the impact of self-organization, the individuality of separate individuals in the group can manifest itself more definitely than in isolation (Hemelrijk and Wantia, 2005). On the other hand, the necessity of reaching a consensus can induce individuals "to give up" clearly defined individual behavior and follow the general strategy of the group (Sumpter et al., 2008). It is known that bolder individuals act as leaders in groups of some bird species (Beauchump, 2000; Kurvers et al., 2009). This agrees with the data obtained by Swedish researchers on the perch (Magnhagen and Bunnefield, 2009). The boldness level of the given species was studied in isolation and in groups of conspecific individuals. The fish in these tests were usually shyer in isolation than in the group. However, the boldness level in the boldest individuals did not change, which made them potential leaders of the group. Actually, a study of the team behavior and leadership in three-spined sticklebacks (Harcourt et al., 2009) demonstrated that bold individuals demonstrated initiative to a greater degree, while other individuals exerted a relatively small impact on their behavior. Moreover, when other fish followed bold individuals, the bold fish increased their tendency for leadership at the expense of the mechanism of positive feedback. All of this made bold sticklebacks leaders of the group.

In addition to individual experience and social environment, individual characteristics of fish behavior can also be influenced by different physical factors. One of the most important factors for fish, as for other exothermal animals, is the environmental temperature, which considerably affects metabolism. Actually, even a slight temperature change is capable of considerably affecting the boldness and aggressiveness of moonies *Pomacentrus moluccensis* and *P. bankanensis* (Biro et al., 2010). It is of interest that correlations between the behavior of individuals in different situations were stable upon a temperature change; however, separate individuals differed by their degree of flexibility. While some fish considerably increased activity upon atemperature increase, others demonstrated a more pronounced stability of their individuality and did not change activity under these conditions.

Thus, most characteristics of individuality are not strictly genetically fixed. They are influenced by the conditions in which early ontogeny passed, physical environmental conditions, and individual experience. The social medium is capable of seriously modifying the temperament characteristics of fish, and, in turn, the temperament of separate individuals considerably affects (and in some cases forms) the social structure of the group. It is also of interest that the degree of flexibility of behavior and its susceptibility to environmental impacts and experience—individual flexibility and a capacity for learning—can by themselves be individuality characteristics. Individual flexibility and a capacity for learning can be related to other individuality characteristics (such as boldness) and supported by natural selection (Dingemanse et al., 2010).

ADAPTIVE IMPORTANCE OF INDIVIDUAL DIFFERENCES IN BEHAVIOR

Early ecological models of communities ignored individual differences in behavior, regarding them as a nonadaptive variation around a definite "norm." However, already in the 1990s, models and alternative strategies, individual differences, and the temperament of animals began to be considered. As a statistical meta-analysis of published data performed by American researchers (Smith and Blumstein, 2008) showed, stable characteristics of individuality, such as boldness and aggressiveness, exert a considerable effect on the final adaptation of individuals of different taxonomic groups of animals, including fish. Thus, it is reasonable to suggest that individual differences in behavior are adaptations formed under the action of natural selection.

In the work of Wilson et al. (1994), a relatively simple model was suggested based on the concept of frequency-dependent selection to explain the coexistence of shy and bold individuals in a population colonizing two biotopes—dangerous and safe. In this case the optimal behavior of an individual depends on the frequency of alternative behavior types in a population. For instance, fearfulness can be most adaptive for each individual, so that at the initial stage they manifest fearfulness, colonizing solely safe biotopes. However, when the density of such shy individuals in the biotope begins to exceed a particular level, this biotope becomes overpopulated. At some moment the competition level in a safe biotope begins to exceed the risk of predation related to entering a dangerous biotope. At this moment some individuals begin to exploit the latter, manifesting boldness. With an increase in the population density, the attractiveness of the dangerous biotope increases. Thus, if populations exploit several biotopes, resource types, subniches, etc., natural selection is capable of supporting stable individual differences at the expense of the mechanism of frequency-dependent selection and individual specialization (Wilson, 1998).

The results of research on fish in many cases correspond to the given model. For instance, in the work of Budaev (1997a), considerable individual differences in the degree of shyness–boldness were revealed in Black Sea wrasses. Bold individuals preferred dangerous open biotopes and were distinguished by poorly pronounced team behavior. Shy fish, as a rule, preferred to be in groups of conspecific individuals near thickets rich in shelters. Similar results were also obtained for the common sunfish *Lepomis macrochirus* and *L. gibbosus* (Ehlinger and Wilson, 1988; Wilson et al., 1993), the bold and shy individuals of which also differed by biotopic preference and team behavior in a similar way. Moreover, shy and bold sunfish also differed by food composition, which indicates that they could exploit different subniches. It is important to note that food specialization and the alternative tactic of food foraging behavior, which are related to use of several alternative resources, biotopes, or substrates (in a heterogeneous medium), have long been known in fish (Bryan and Larkin, 1972; Ringler, 1983; Smith and Skúlason, 1996; Kasumyan and Sidorov, 2002; Mikheev, 2006).

More complex adaptive models are based on the use of dynamic programming when the adaptation of each type of behavior is counted iteratively and depends on the state of an individual, including energy resources, territory size, and other factors (Mangel and Clark, 1988). It is possible to construct relatively simple models that predict the presence of consistent individual differences and the coexistence of individuals with different behavior types when the state of an individual and the history of its behavior (individual experience) over time are considered (Dall et al., 2004). For instance, stable individual differences in the inclination for risk can be supported by selection when individuals differ by their energy reserves and these differences are not smoothed out by environmental factors (Dall et al., 2004; Rands et al., 2003). Another important factor causing an increase in the stability of individual differences is environmental uncertainty, as well as accidental fluctuations in it (McErleah and Strimling, 2006). Actually, under conditions of uncertainty, it may turn out that it would be more profitable for individuals differing by their state (body size, hormonal characteristics, individual experience, etc.) to use fixed strategies rather than to make considerable efforts to assess and precisely predict environmental factors.

Adaptive trade-offs between different types of behavior are yet another adaptive mechanism promoting the appearance of stable individual strategies (Stamps, 2007; Biro and Stamps, 2008). For instance, Wolf et al. (2007) elaborated a model based on the conflict between the probabilities of current and future reproduction. According to this model, individuals expected to have a high reproductive success that "have something to lose" are characterized by shyness, while individuals with a low expectation should be bolder. Actually, in this case we deal with the more general Clark "asset protection principle" (Clark, 1994), which asserts that the higher the current magnitude of the accumulated reproductive asset, the more important is the avoidance of a risk threatening reproduction. Thus, the accumulation of a reproductive asset (increase in body size, territory size, etc.) should in general case lead to risk avoidance.

Adaptive conflicts between growth and mortality (Stamps, 2007) or between reproduction and mortality (Biro and Stamps, 2008) represent important mechanisms that explain the existence of consistent individual differences in behavior. Models based on such a mechanism postulate that correlations between the behavior of individuals in different situations forming general boldness (as other similar temperament characteristics of) arise when they affect growth, reproduction, and mortality. Actually, many fish, as well as other animals, demonstrate consistent individual differences in the rate of growth and reproductive success (Biro et al., 2006; Stamps, 2007). Behavioral characteristics related to the tendency for risk and aggressiveness frequently affect both the rates of growth and mortality. Boldness and aggressiveness accelerate the growth rate, facilitating the obtainment of access to a food resource, and frequently increase reproductive success (especially in males (Godin and Dugarkin, 1996)). However, they also increase the risk of being eaten by a predator and sustaining an injury. Under these conditions one can expect a wide range of behavioral types, since nether of them is solely optimal. In the more general case, any adaptive conflict between characteristics of the life cycle strategy can promote support by the selection of consistent individual differences in behavior, since the most diverse behavioral tactics and temperament types have a similar adaptation in this case (Schluter et al., 1991; Wolf et al., 2007; Biro and Stamps, 2008).

An adaptive conflict between the rate of decision-making and its accuracy can lead to the emergence of individual differences in impulsiveness. For instance, some individuals can be distinguished by a tendency for rapid decision-making; however, they base decisions on a rather rough environmental estimate. Other individuals, conversely, make decisions slowly, basing them on the maximum complete information (Chittka et al., 2009). As it turned out, guppy individuals are characterized by consistent individual differences in the extent of their "impulsiveness" when taught in a spatial labyrinth: some of them are inclined to get trained and make rapid decisions but with a great number of errors. Other individuals are trained slowly, but make fewer mistakes (Burns and Rodd, 2008).

An adaptive conflict between the need to provide food for progeny and the accumulation of individual experience by juveniles leads to the coexistence of a considerable individual variability of parental behavior in the convict cichlasoma *Archocentrus nigrofasciatus* (Zworykin et al., 2000). A high level of parental contribution in this case increases the accessibility of high-quality food for juveniles. However, on the other hand, a weak level of provision with food stimulates juveniles to independently learn to get food. The result of this adaptive conflict is the coexistence of a wide range of nearly equal adaptive strategies, in which some parents actively provide food to progeny while other parents do not.

Still another important mechanism promoting selection support of consistent individual differences is social behavior, as well as all kinds of social conflict that offer possibilities for individuals to take on different social roles. In this case specialization in particular social niche entails the use of correlated social, ecological, and behavioral tactics, jointly forming a unique integrated complex or a syndrome (Bergmüller and Taborsky, 2010). For instance, the midas cichlid *Neolamprologus pulcher* lives in colonies consisting of individuals with different social roles. Some of them reproduce, while others (helpers) do not participate in reproduction but rather support the normal state of the nest, participate in the care of progeny and defense from predators, etc. Individuals that perform different social roles considerably differ by a multitude of behavioral characteristics, including boldness, aggressiveness, and preference for team behavior, which include temperament characteristics (Witsenburg et al., 2010; Chervet et al., 2012; Riebli et al., 2011, 2012).

In social situations individuals can obtain information on the history of cooperative behavior (for instance, mutual aid). As the model elaborated by McNamara et al. (2009) shows, natural selection in such cases can promote the manifestation of the "social consciousness" of individuals, which in turn supports consistent individual differences of those characteristics that are subjected to social monitoring or related to it. This mechanism can be important not only for species characterized by rather complex social relations and social structures, such as primates, but for fish as well. Actually, it is long known that fish manifest cooperative behavior, including the reciprocal type (Milinski et al., 1990; Dugatkin and Alfieri, 1991; Dugatkin and Mesterton-Gibbons, 1996). In addition, more and more data have appeared showing that fish are capable of forming rather complex social networks (Croft et al., 2004; Pike et al., 2008; Croft et al., 2009).

Thus, natural selection can form consistent individual behavioral characteristics. The most general mechanisms promoting their appearance are frequency-dependent selection and adaptive trade-offs between different behavior types. The use by individuals of several biotopes, resource types, or subniches can considerably increase the consistency of individual differences in a population. Environmental heterogeneity is a key mechanism leading to coexistence within a population of a multitude of alternative strategies of behavior (Mikheev, 2006). Important mechanisms promoting coexistence within a population of individuals with different temperament characteristics include accidental environmental fluctuations, individual experience, social relations, etc. (Dingemanse and Wolf, 2010; Dall et al., 2004).

EFFECT OF INDIVIDUAL DIFFERENCES ON POPULATION DYNAMICS

Although the differences between populations of fish in many behavioral patterns are rather well studied (Bell and Stamps, 2004; Dingemanse et al., 2007), the role of individual differences in population processes is unclear in many respects. Nevertheless, it is known that the presence of individuals with different characteristics can considerably affect population processes. For instance, intrapopulation variability according to traits such as growth rate, body size, etc. can support population stability (decreases the range of stochastic fluctuations) and increase consistency for extinction upon the onset of catastrophic events (Lomnicki, 1988; Uchmanski, 2000; Grimm and Uchmanski, 2002). Traditional models of population dynamics consider individual variations of morphological traits and characteristics of the life cycle strategy. However, they can also involve behavioral variability, especially if the latter is related to competitiveness, use of resources, and life cycle strategy (Biro and Stamps, 2008).

Individual variation can promote the coexistence of competing species. For instance, a rather simple model based on a modification of the Lotka-Volterra equation (Begon and Wall, 1097) demonstrates the importance of individual differences for the support of the coexistence of two competing species. In a classical model without individual variation, the more competitive species rapidly dominates, dooming the competitor to extinction. However, the presence of individual differences in both competing species leads to their coexistence.

Research on the effect of consistent individual behavioral differences on population processes remain rather rare. In one model (Petrovskii et al., 2008), a population in a homogeneous environment under favorable conditions is considered. At some moment, a catastrophic degradation of conditions occurs, which causes fragmentation of the population and considerable mortality. It turns out that the addition of consistent individual differences in behavior (the same individuals manifest only aggressive or nonaggressive behavior independently of the context) leads to a considerably smaller decrease in the population density than in case when individuals are inconsistent (can freely switch between aggressive and nonaggressive behavior).

In the work of Budaev et al. (1999b), a considerable assortativeness in the formation of couples in individuals of convict cichlasoma was revealed; in successfully reproducing couples, males and females were characterized by similar boldness levels. Couples that did not demonstrate assortativeness formed; however, with time they came apart without spawning. A recent study on the guppy (Ariyomo and Watt, 2013) demonstrated that reproductive couples formed of individuals strongly differing in boldness (disassortative) were distinguished by decreased reproductive success. Similar assortativeness arises as a result of sexual selection and has a considerable effect on the population structure, being an important mechanism of sympatric species formation (Johnson et al., 1996; Kondrashov and Shpak, 1998). All of these results indicate that consistent individual differences in behavior, behavioral syndromes, and temperament are an important, though underestimated, component of biodiversity (Pavlov and Bukvareva, 2007; Budaev and Brown, 2011).

CONCLUSIONS

Intrapopulation variation and alternative strategies of social, reproductive, feeding, migrational and other kinds of behavior are currently well described in the literature (Magurran, 1993; Conrad et al., 2011; Budaev and Brown, 2011). A rather considerable part of general behavioral variation is related to individuality. Our analysis demonstrates that consistent individual differences in individual behavior are of great ecological importance. Individuality characteristics affect taste preferences (Kasumyan and Sidorov, 2002) and specific features of feeding (Mikheev and Wanzenböck, 1999), the preferred use of biotopes (Mikheev and Pasternak, 2005), distribution, migrations (Pavlov et al., 2007), susceptibility to parasites and diseases (Barber and Dingemanse, 2010, electrocommunication (in weakly electric fish Kasumyan et al., 2013), and many other aspects of fish ecology. The boldness–shyness continuum thus seems to be particularly important, since the adaptive significance of different behavior types in situations related to risk (for instance, predation) is most often obvious. Therefore, it is not surprising that the given continuum, as several other characteristics, manifested in situations of risk were studied the most completely (Sih et al., 2004a; Budaev and Brown, 2011; Conrad et al., 2011). Despite this, many other aspects of individuality may turn out to be no less important for understanding many processes occurring in populations. Although populations are frequently regarded as homogeneous, recent research more and more casts doubt on such an opinion. Moreover, the intrapopulation diversity of behavioral strategies and characteristics represent a major component of biodiversity that also needs preservation (Pavlov and Bukvareva, 2007; Budaev and Brown, 2011). Individuality characteristics, structure, and plasticity level are separate complex phenomena requiring further studies.

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