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"Personality" in the Guppy (*Poecilia reticulata*): A Correlational Study of Exploratory Behavior and Social Tendency

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Differences in the exploratory behavior and social tendencies of 29 guppies (*Poecilia reticulata*) in 2 domains of situations involving novelty and conspecifics were investigated. Consistent individual differences were found in most behavior patterns. Two behavioral dimensions (Activity Exploration and Fear Avoidance) were identified in the novelty situations. Likewise, 2 dimensions (Sociability and Locomotion) were found in the social situations. An analysis of relationships between these 2 test domains revealed the existence of even broader behavioral dimensions (Approach, governing exploration and social attraction, and Fear Avoidance, governing responses to aversive stimulation). Thus, it was shown that "personality" may represent an important behavioral category in the guppy provided it is defined precisely and objectively.

Comparative psychologists and ethologists have always been interested in the study of animal temperament (e.g., Hall, 1941; Stevenson-Hinde, 1983; Tryon, 1942) and adaptive individual differences (Clark & Ehlinger, 1987; Magurran, 1993; Slater, 1981). Some of the reviews (Budaev, 1996; Clark & Ehlinger, 1987; Eysenck & Eysenck, 1985; Stevenson-Hinde, 1983; Wilson, Clark, Coleman, & Dearstyne, 1994) emphasized the importance of studying integrated behavioral phenotypes and stable traits that are consistent over time and across situations, that is, temperaments and personalities. Therefore, broad and consistent dimensions of individuality represent an integrative framework for the studies of individual differences. Thus, one can speculate about "personality" or "temperament" in animals without any impression of anthropomorphism provided it is defined objectively and precisely (Budaev, 1996; Francis, 1990; Mather & Anderson, 1993; Stevenson-Hinde, 1983).

Because the distinction between personality and temperament is somewhat vague and the latter term typically has a more restrictive meaning (e.g., involving only early developing traits or stylistic, temporal, and dynamic traits as distinct from the content and motivation; see Budaev, 1996; Eysenck & Eysenck, 1985; and Zuckerman, 1994, for more exhaustive discussions), I prefer to use the word *personality* to designate consistent individual differences in fish. At least, one can argue that animals may have temperaments that are molded into adult personalities by experience (Mather & Anderson, 1993).

The main aim of the present study was to determine the basic motivational systems and corresponding personality dimensions as revealed in situations involving exploratory, predator inspection, and schooling behavior in the guppy (*Poecilia reticulata*). If personalitylike traits do really exist in this species, it should be possible to show that (a) individual differences are both consistent over time and across situations, (b) these differences can be organized into a small number of dimensions, and (c) these dimensions could be meaningfully interpreted in motivational terms. I also tried to establish whether the interindividual variation is continuous or whether there exist alternative strategies, such as the alternative coping styles found in mammals (see Benus, Bohus, Koolhaas, & Oortmerssen, 1991). Finally, I attempted to ascertain whether the consistent personalitylike traits interact with a standard sampling procedure whereby individuals are selected from a larger pool; if yes, this may pose a serious methodological problem.

The guppy is a particularly appropriate species for this sort of studies because various aspects of its biology and behavior have been studied quite well. In addition, this species demonstrates a fascinating between-populations variation in many behavioral and morphological traits (Magurran, 1993; Magurran & Seghers, 1990; Magurran, Seghers, Carvalho, & Shaw, 1992). Several inbred strains of guppies have also been developed (J. H. Schröder, personal communication, August 17, 1995). The situations of inspection and exploratory behavior were selected as the basis for the present investigation because they involve complex interactions between opposing tendencies and require decision making in the situation of obvious tradeoff: to explore a novel environment, to flee, or to freeze. Therefore, it was expected that specific motivational systems might be identified, acting simultaneously to produce the overt behavior. In addition, inspection behavior plays an important role as a predator-avoidance mechanism in the natural environment (Dugatkin & Godin, 1992; Magurran & Girling, 1986) and

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differs thoroughly with other behavioral variables in relation to predator pressure in particular habitats (Magurran & Seghers, 1990; Magurran et al., 1992). Finally, novel environments and predators represent stressful situations, and it was suggested (e.g., Gerlai & Csányi, 1990; Suomi, 1983) that individual differences become more stable and predictable under mild stress.

Method

Subjects

Experimental subjects were guppies (*Poecilia reticulata*) obtained from a feral population of unknown origin in Moscow, Russia. This population has been living for more than 20 years in a warm water stream commencing from the sewage purification station Nizhniye Polya and falling into the Moscow river. The water was too turbid to perform any detailed observation on the behavior of guppies in this environment. However, the fish formed well-developed schools and demonstrated a high tendency to avoid any human standing at the side of the stream. In addition, a majority of captured male guppies had relatively inconspicuous wild-type coloration often characteristic of guppies living in the wild in Trinidad.

Following initial capture from the stream, about 100 fish were maintained for 1 week in a large, round rearing tank 0.9 m in diameter and 0.3 m in depth. During this period they were exposed to a short (2 days) streptomycin prophylactic against possible diseases.

Later, 29 adult male guppies (standard length = 1.6–2.0 cm) were selected from this larger group in a sequential way with a small hand net (10 ×15 cm, with the handle 30 cm long), and the order of capture was written down. Each fish was measured, weighed, and transferred into housing aquaria. Only male guppies were studied during the present investigation because the behavior of female guppies fluctuates profoundly in relation to ovarian cycle (Warren & Callaghan, 1976).

The fish were maintained individually in 100-L tanks divided by opaque partitions into 12 small compartments. Temperature was held constant at 22–24 °C. Fish were reared with a 12-hr photoperiod (20 lx illumination at 10 a.m. to 10 p.m.) and were fed every day with a commercial flake food. Occasionally, live *Tubifex* worms, small *Chironomidae* larvae, and *Daphnia* were also given. Fish were left to adapt to the laboratory conditions 2 weeks before the experiments started.

Tests and Procedures

Observations. Four tests with multiple trials were administered to every subject with approximately 1 month between test periods as described below. In each trial of a particular test, the fish were selected in a randomized order to prevent sequential artifacts. Temperature and the level of illumination in all tests were held exactly the same in experiments as in the housing aquaria to attenuate stress. All observations were conducted directly through a small window in a screen separating the experimental apparatus from the observer to prevent disturbance of the fish.

During the observations, specific behavioral activities described below were recorded on an audiocassette recorder. Consequently, the records of the observer's comments were coded onto a personal computer by cassette playback using a specially written software (Budaev, 1995) that accepted keystrokes as codes for particular behavioral patterns. Only the percentages of the total duration spent displaying specific behaviors were analyzed in the present article, which correlated with respective frequencies.

Open-field test. An open-field test was performed in 3 consecutive days in a hexagonal tank 0.9 m in diameter, with the water level at 9 cm. A coordinate grid (10 × 10 cm) was marked on the bottom of the tank to record the locomotor activity.

Initially, a guppy was gently released into a white bottomless opaque plastic cylinder (the start box) for 2 min to ensure that it acclimated after the handling. After that, the cylinder was lifted, and the behavior of the fish was observed from above for 5 min. Behavioral items recorded included the number of squares crossed and the total percentage of duration spent moving (MOVE). The former variable, called *ambulation score*, is probably the most common in studies of laboratory rodents (Archer, 1973; Walsh & Cummins, 1976) as well as fish (e.g., Gervai & Csányi, 1985; Warren & Callaghan, 1976). Instead of the raw number of crosses, I calculated the rate-per-minute observation of ambulation, which is referred to hereinafter as AMB.

Predator inspection test. The inspection test apparatus was an aquarium (60 × 30 × 20 cm) with three compartments (see Figure 1). The home compartment was separated from the inspection compartment by an opaque partition with a sliding door (6 × 6 cm; at 1 cm above the floor), whereas the predator compartment was located behind a transparent glass wall. The predator compartment contained a convict cichlid *Cichlasoma nigrofasciatum* (l = 7.8 cm) "predator," placed into a V-like white plastic fold to prevent it from hiding in a corner. This cichlid was maintained in this compartment for 2 days before the experiment and all subsequent period of testing (but without the fold, which was installed 15–20 min before testing). The cichlid was fed 1 hr before the experiment, was relatively inactive, and did not direct any predatory attack toward the tested guppy.

The test was performed on 3 consecutive days in the following way. An individual guppy was gently transferred into the start box placed into the home compartment with the door closed. The fish was given 2 min to recover from capture and transfer, the box was elevated, and the behavior of the fish was observed for 5 min (first subtest). The door was then opened and the behavior recorded again (second subtest) until the subject entered the inspection compartment. The cutoff time allowed for entry was set to be a random variable within 4–6 min. In case the fish did not enter at all, it was again placed into the start box standing directly in the inspection compartment. The latency to enter, therefore, was a

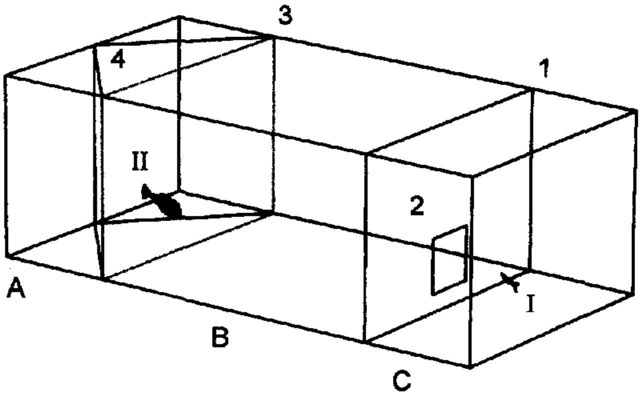

Figure 1. The inspection test apparatus. The tank consisted of predator (A), inspection (B), and home (C) compartments. 1 = opaque partition with a sliding door (2); 3 = glass partition; 4 = V-like fold; I = tested fish; II = cichlid.

randomly censored variable. As soon as the individual entered the inspection compartment, the third subtest began and continued for 5 min.

Behaviors recorded during all three subtests included the following: STOP: motionless, hanging in midwater; FRZ: freezing at the bottom; SKI: skittering, that is, a series of rapid darts; MOVE: movements over the experimental tank (as in the open field); ESC: attempts to escape through glass walls of the test aquarium. Also, during the third subtest in which guppies were confronted with a cichlid, predator inspection visits (INSP) were recorded. These were defined as apparent approaches to the predator compartment followed by more or less prolonged visual fixations on the cichlid occupying it (Magurran & Girling, 1986; Magurran & Seghers, 1990). Because other behaviors like pecking and extremely slow or quick swimming took small proportions of time, were not observed consistently in all subjects, and were not regularly correlated across test exposures, they were not included in the present analysis. Although the convict cichlid is not a natural predator of the guppy, a number of visually similar cichlid predators are sympatric with many guppy populations in Trinidad (Reznick & Endler, 1982).

Schooling tendency test. The schooling tendency test was performed twice with a 2-week between-trials interval in the same tank as the inspection test, but with the fold removed, the home compartment blocked, and the cichlid replaced by a group of 4 conspecific male guppies.

An individual subject was released into the start box for 2 min, after which the latter was lifted and the fish was observed for 10 min with STOP, FRZ, SKI, MOVE, and ESC units recorded as in the previous test. Attempts to enter the compartment with conspecifics (ATMPT; that is, looking similar to escape, though typically less fierce and directed to the compartment with conspecifics rather than to any other wall, as if the fish attempted to "go through" the glass) were also taken.

Mirror test. The mirror test apparatus was an aquarium measuring 36 × 30 × 20 cm with a mirror (30 × 20 cm) attached to one wall. The procedure of testing was similar to that in the previous test with the behaviors STOP, FRZ, SKI, MOVE, and ESC recorded again. Attempts to get through the mirror (MIRR), phenomenologically similar to ATMPT, and direct visual fixations on the mirror image while hanging in midwater in close proximity to the mirror (LOOK) were recorded as well. This test was administered to the guppies twice, separated by a 2-week interval.

During the second trial of testing, 1 fish was inadvertently disturbed and consequently was omitted from all statistical analysis procedures involving data aggregation. Thus, a sample size of 28 instead of 29 occurred in some cases.

Extraction of Personality Dimensions

The numerous measures scored in the above tests yielded up to 83 behavioral parameters for each individual guppy. Therefore, I performed a series of consecutive steps to arrive at a much smaller set of only the most salient personality dimensions. It would be much simpler to perform a single factor analysis on all these variables; however, small sample size and the highly unsatisfactory variable-to-subject ratio (83/29!) would certainly lead to a highly unstable correlation matrix. That is why I decided to use this much more complex stepwise strategy, concentrating at each step on more and more broad behavioral domains: first, determining whether individual behavioral measures are consistent and reliable; second, establishing whether they form some clusters within the domains of situations (novelty predator and conspecifics); and third, revealing the higher order clusters of behaviors that appear between these domains.

Step 1: Reliability analysis and data aggregation. First, I proceeded with data aggregation (Epstein, 1983) to reduce the large number of variables to a manageable and interpretable number with the aim of representing most economically individual differences in important behavioral domains. One virtue of data aggregation is that it usually has the same effect as increasing the sample size (by canceling out random variation and measurement errors; see Epstein, 1983) and decreases the probability of large instability of the correlation matrix. Reliability analysis, or examining the degree to which multiple variables shared a common portion of variance, took place before the aggregation to avoid possible obscuring of independence between measures. Thus, I computed Pearson correlation coefficients, Cronbach alphas, and Spearman-Brown split-half reliability coefficients (Nunnally, 1967) for the sets of variables representing particular behavior units. These were based on the correlations calculated for the same behaviors across exposures of each test and subtest. This method of data reduction and analysis is commonly used to construct psychological tests and questionnaires (Nunnally, 1967), and there exist some examples of its successful application in the study of animal behavior (Maier, Vandenhoff, & Crowne, 1988; Ossenkopp & Mazmanian, 1985; Tachibana, 1985). Because the latencies to enter the inspection compartment were censored and therefore unsuitable to standard correlation and reliability analysis, I used an extension of the Spearman's correlation test for this sort of data (Krauth, 1988).

Step 2: Principal-components analyses. Ten variables that survived the data reduction procedure and originating from the open-field and inspection tests were subjected to principal-components analysis (Stevens, 1986). Furthermore, 11 composite variables originating from the schooling and mirror tests were subjected to this type of analysis too. Thus, two distinct components analyses aimed at establishing the structure of the dimensions underlying the behavioral variation between subjects were performed separately. The scores of each fish on the principal components were also computed for use at the subsequent steps of data analysis.

I also conducted the common factor analysis (with multiple R^2s as initial estimates of communalities). Because both methods yielded virtually the same results and conclusions as the (simplest) component analysis, I do not report the factor analysis here. However, it is worth noting that the results of factor and principal-components analyses often depend markedly on the methods used; furthermore, random variation and measurement errors may produce spurious factors that could often be "meaningfully" interpreted (Armstrong & Soelberg, 1968). The high invariance of results with respect to the method, however, represents important evidence for the stability and validity of factors.

Although an orthodox and conservative rule of thumb (e.g., Nunnally, 1967) demands hundreds of subjects and the stringent variable-to-subject ratio of 1:10 for any multivariate analysis to be valid, several studies established that the factor stability may be achieved with much smaller sample sizes and with a variable-to-subject ratio of 1:3 (Baggaley, 1982). Furthermore, reliable aggregated variables were used in the present analysis instead of possibly unstable original scores (in a sense, this led to a "sample size" equivalent to 29 fish × 3 test exposure = 87 "cases" or even 29 × 6 = 174 "cases"). All this made the possibility of unstable correlation matrix unlikely. Factor loadings greater than .5 were considered interpretable.

The most important point for the present investigation was the proper number of higher order behavioral constructs to extract. Given a particular domain of variables, is it better to extract a few broad factors or a larger number of narrow ones? I approached this matter cautiously by computing a series of rotated solutions and attempting to retain those factors that appeared in all of them. I also inspected the Kaiser's root-one solution, the Cattell's scree test, and the very simple structure (VSS) goodness-of-fit test (Revelle & Rocklin, 1979) to base the decision about the number of factors on several independent tests.

The initial factor pattern matrices were subjected to the Kaiser's normalized varimax rotation, which typically gives good separation of orthogonal factors. I also tried several other orthogonal and oblique rotations, but the results were similar.

Because the latencies to enter the inspection compartment were censored, there was no direct way to correlate them with other variables and thereby include them in the principal-components analysis. Specialized regression analysis, however, exists in the context of survival analysis that is applicable to the censored observations (Lee, 1992). Among a variety of possible models, the Cox proportional hazard model is especially appropriate to the data because it is basically nonparametric. Thus, the scores of each individual guppy on the first two principal components were regressed with the latencies to enter the inspection compartment during the first, second, and third exposure, which resulted in three distinct regression analyses. I considered as interpretable (significant) only the effects for which the absolute t values (equal to the regression weights divided by their respective standard errors) exceeded 2.

Step 3: Canonical correlation analysis. In the final step of data analysis, I attempted to determine putative common dimensions underlying the behavior of guppies in all the situations studied during the present investigation. Thus, canonical correlation analysis (Stevens, 1986) was conducted to elucidate the relationships between the principal components based on the open-field and inspection tests, on the one hand, and the composite (aggregated) measures based on the schooling and mirror tests, on the other.

Two essential questions, which cannot be answered by simple correlation or regression analysis, were dealt with at this stage of data analysis. First, how many dimensions were necessary to represent the relationships between the variables and components? Second, given the relationships, to what extent were the dimensions univocal representations of the principal components (i.e., whether each correlated with only one principal component or was an amalgam of both)?

In fact, several canonical and factor analyses were performed for various subsets of measures; however, all of these led to virtually the same conclusions (really implying stability and validity of the personality dimensions) and are not reported here. As any other multivariate analysis, canonical analysis demands a relatively large sample size. However, the considerations on this matter discussed with respect to the component analysis hold here too, as far as low canonical correlations are not considered, the number of variables is not too large in relation to the number of individuals, and intradomain collinearity is not high (Stevens, 1986). The dimensionality of the relationships was tested using chi-square test based on the lambda statistic. I judged the canonical loadings greater than .5 as interpretable.

Analysis of Discontinuous Variation

I inspected the normal probability plots of each original variable for nonnormality and discontinuous variation. In case of the latency to enter, survival curves based on Kaplan-Meier estimates (Lee, 1992) were analyzed. I also fitted exponential distributions to the latencies (which implies an overtly random decision to enter the novel area). Hierarchical cluster analysis was also used to confirm the groupings revealed by the univariate analysis. I used Ward's minimum variance algorithm (Stevens, 1986) with Euclidean distances computed on standardized scores. This approach typically gives the most accurate results in finding the "true" underlying cluster structure and is widely used by psychometricians.

One may question the validity of establishing multimodal variation on the basis of a relatively small sample size (29 fish), because even with a sample size greater than 100, a bimodal pattern may not be obvious (Biro & Ridgway, 1995; McLaughlin, Grant, & Kramer, 1992; however, both are field studies that do not control the within-individual variability). This also made it impossible to fit a combined distribution to the data. Furthermore, the fact that the latency to enter was a censored variable further limited its statistical treatment. On the other hand, I analyzed highly consistent variables (particularly freezing, with the reliability coefficients about .8, see below), and therefore random variation and measurement errors were unlikely to increase or confound the overall scatter. Thus, I judged whether bimodality took place on the basis of simple visual inspection of distribution patterns. Such an approach is typically followed, for instance, in cluster analysis and multidimensional scaling, in which exact significance tests do not exist.

To establish the validity of the two personality dimensions (see Results section), I repeated exactly the same steps of multivariate analysis (principal-components analysis and canonical correlation analysis) separately for the fish characterized by low freezing scores, that is, for nonfreezers only (see Results). However, a smaller subset of only the most reliable composite behavioral indexes was analyzed here. It was dictated by the reduced sample size ($N = 19$), requiring a minimal variable-to-subject ratio for the analysis to be statistically correct.

Sequential Sampling Bias

To ascertain whether guppies have been initially caught randomly from the large rearing aquarium (containing 100 subjects, see above), I inspected sequence charts for the two principal components (Activity Exploration and Fear Avoidance; see Results) and calculated the Spearman's correlation coefficients between particular variables and their consecutive indexes. In case of the censored latency measures, composite latency scores (Theobald & Goupillot, 1990) were calculated before the analysis.

Details of Statistical Tests

All statistical significance levels reported are two-tailed. Effects with $p < .05$ were considered significant. With $N = 29$, a correlation equal to .36 is significant and the power to detect a correlation of .5 (accounting for 25% of variance) is equal to .80. This study represented an exploratory correlational analysis rather than testing a compound hypothesis, in which significance in any individual test would lead to its complete rejection. Therefore, the possibility of a Type I error inflation was not taken into account (Wright, 1992), and no adjustment of the p values was made. Beyond this, however, in most cases the p values turned out to be adequately low (often less than .0001), stable composite measures were analyzed instead of unreliable original scores, and virtually the same patterns appeared after the analysis of a different data subset (see the analysis of discontinuous variation). Furthermore, for most families of tests, the largest p value was significant, which means that with the Hochberg's procedure, no adjustment was needed (see Wright, 1992, for an overview). Because of the large number of relationships analyzed, treating all of the tests as a single family would result in inferences that are far too conservative.

Table 1
Reliabilities of the Measures Scored in the Open-Field and Inspection Tests

Variable	α_1	α_2	Split half	α_{1+2}	α_3
Open-field test					
AMB	.90				
MOVE	.89				
Inspection test					
FRZ	.84	.80	.94	.91	.70
STOP	.68	.63	.85	.80	.51
MOVE	.89	.81	.91	.91	.84
ESC	.78	.76	.93	.89	.74
SKI[a]	.25	.03	.30	.28	.00
INSP[a]					.24

Note. See text for full definitions of behaviors. α_1 denotes the Cronbach alpha reliability coefficient for the first, α_2 for the second, and α_3 for the third subtest, each containing three items. α_{1+2} represents the reliability of a pooled set, including both first and second subtests (six items). Spearman-Brown split-half reliability coefficients between the first and second subtests are also included (Guttman coefficients showed similar values).

[a] Inferior reliabilities caused by low and nonsignificant correlations between items.

Results

Neither length nor weight of individual guppies correlated significantly with either behavioral measure analyzed in this study; the vast majority of correlations closely approached zero (with the p values ranging from .5 to .9).

Extraction of Personality Dimensions

Step 1: Reliability analysis and data aggregation. All behavioral parameters measured were highly correlated between trials (see Tables 1 and 2). The STOP scores were slightly less consistent. Split-half reliability analysis confirmed increasingly large consistencies between the sets of the measures scored in the first and second subtests of the inspection test. As a result, the reliabilities of the pooled sets of items were reasonably high. However, the percentages of time spent inspecting the predator and skittering were not consistent across trials.

Table 2
Reliabilities (Pearson Product-Moment Correlations) of the Measures Scored in the Schooling and Mirror Test

Variable	r	p
Schooling test		
FRZ	.76	.000
STOP	.50	.006
MOVE	.59	.001
ESC	.59	.001
SKI[a]	.32	.103
ATMPT	.75	.000
Mirror test		
FRZ	.84	.000
STOP	.51	.006
MOVE	.81	.000
ESC	.59	.001
SKI[a]	.18	.374
LOOK	.61	.001
MIRR	.81	.000

Note. See text for full definitions of behaviors.

[a] Low and nonsignificant ($p > .1$) correlations.

Thus, a majority of the behavioral measures scored were consistent and repeatable across trials despite possible changes in their absolute levels. Therefore, it was possible to construct the composite scales representing individual differences in important aspects of the guppy behavior. The variables that proved to be fairly reliable and consistent were aggregated for further analysis.

Predator inspection visits were inconsistent across all three test trials, and this can be understood from a closer analysis of the pairwise relationships between the trials. Although the first trial INSP score did not correlate with the second ($r = -.008$, $N = 29$, $p = .967$, *ns*) or with the third ($r = -.005$, $N = 29$, $p = .978$, *ns*), the latter two correlated closely ($r = .868$, $N = 29$, $p < .001$). Thus, the inspection behavior in the guppy is likely to be bifactorial: There might be an exploratory inspection of an unknown predator and a surveillance inspection of a familiar one. Although the INSP score measured in the first exposure reflects a basic tendency to explore the predator, which is typically diminished when the latter becomes more explored (called *habituation of predator inspection;* see Huntingford & Coulter, 1989; Magurran & Girling, 1986), the scores of 5 guppies increased rather than decreased in the second trial. Further detailed analysis suggested that the maximum score would provide a better scale for the measurement of the basic inspection incentive in these timid guppies. Thus, this maximum inspection score instead of an aggregated score was retained for use at the succeeding steps of the data analysis. In addition, because the STOP scores proved to be less repeatable in the third subtest ($\alpha = .51$), the exact record corresponding to the trial with maximum inspection was used further.

As for the skittering behavior, no clear pattern emerged. Almost all pairwise correlations were low and nonsignificant ($p > .1$); therefore, skittering was excluded from the subsequent data analysis. Finally, the open-field MOVE score was excluded because it seemed to be redundant for further correlation analysis; the correlation between the aggregated ambulation and this MOVE scores was high ($r = .94$, $N = 29$, $p < .001$). The censored latencies to enter the inspection compartment were also significantly correlated between repeated trials (Krauth's test: Trial 1 vs. Trial 2: $z = 3.56$, $p < .001$; Trial 2 vs. Trial 3: $z = 4.50$, $p < .001$; Trial 1 vs. Trial 3: $z = 3.26$, $p < .001$). Twenty-one composite variables emerged as a result of this data reduction procedure. These are summarized in Table 3.

Step 2: Principal-components analyses. The results of the component analysis of the open-field and inspection test variables are presented in Table 4. Three principal components with eigenvalues greater than unity emerged, which explained 80% of the total variance, and the Cattell's scree test also implied three factors. However, the last component accounted for small proportion of variance, only 11%.

Table 3
List of Composite (Aggregated) Variables That Survived the Data Reduction Procedure

Variable	*n*	Description of the score
Open-field and inspection tests domain		
AMB$_{OF}$	3	Open-field locomotion (ambulation) score
FRZ$_{12}$	6	Freezing in a small novel environment
STOP$_{12}$	6	Stop in a small novel environment
MOVE$_{12}$	6	Locomotion in a small novel environment
ESC$_{12}$	6	Escape in a small novel environment
FRZ$_{3}$	3	Freezing in presence of a predator
STOP$_{Insp}$	1	Stop in presence of a predator
MOVE$_{3}$	3	Locomotion in presence of a predator
ESC$_{3}$	3	Escape in presence of a predator
INSP$_{max}$	1	Predator inspection score
Schooling and mirror tests domain		
FRZ$_{S}$	2	Freezing in presence of conspecifics
STOP$_{S}$	2	Stop in presence of conspecifics
MOVE$_{S}$	2	Locomotion in presence of conspecifics
ESC$_{S}$	2	Escape in presence of conspecifics
ATMPT$_{S}$	2	Attempts to enter the compartment with conspecifics
FRZ$_{M}$	2	Freezing in the mirror test
STOP$_{M}$	2	Stop in the mirror test
MOVE$_{M}$	2	Locomotion in the mirror test
ESC$_{M}$	2	Escape in the mirror test
LOOK$_{M}$	2	Looking at the mirror image
MIRR$_{M}$	2	Contacts with the mirror image

Note. The variables representing two domains of the test situations are listed separately. The *n* depicts the number of scores that make up a particular composite score (i.e., the number of individual items).

Furthermore, different varimax rotations performed on the initial factor pattern matrix for two to four factors gave similar structures. The results of the factor analysis proved to be even less ambiguous; both Root 1 and scree test clearly indicated two factors. In addition, the VSS goodness-of-fit index achieved its maximum value for the two-factor solution, which suggests that two is the optimal number of interpretable factors. Because overfactoring usually leads to less severe errors than underfactoring (Stevens, 1986), I decided to extract three principal components but interpret only the first two. No one residual correlation exceeded .18 (the maximum value acceptable with $N = 29$), indicating that the component solution was satisfactory.

Table 4
Varimax-Rotated Component Loadings: Open-Field and Inspection Test Variables

Variable	Activity Exploration	Fear Avoidance	Not interpreted
Open-field test			
AMB$_{OF}$	.56[a]	.60[a]	−.02
Inspection test			
FRZ$_{12}$	−.76[a]	−.61[a]	.08
STOP$_{12}$	.76[a]	.14	−.27
MOVE$_{12}$	.85[a]	.06	.20
ESC$_{12}$	.03	.93[a]	−.04
FRZ$_{3}$	−.79[a]	−.52[a]	.12
STOP$_{Insp}$	−.10	−.10	−.94[a]
MOVE$_{3}$	.82[a]	.02	.13
ESC$_{3}$	−.05	.92[a]	.19
INSP$_{max}$	.79[a]	−.21	.28
Eigenvalue	4.83	2.08	1.13
Variance accounted (%)	48.31	20.77	11.29

Note. See text for full definitions of behaviors.
[a] Interpretable loadings.

The first principal component was loaded (see Table 4) positively by the locomotor measures (MOVE$_{12}$ and MOVE$_{3}$), predator inspection (INSP$_{max}$), immobility (STOP$_{12}$), and open-field ambulation, but negatively by freezing (FRZ$_{12}$ and FRZ$_{3}$). It was interpreted as Activity Exploration. The second principal component was determined by the attempts to escape (ESC$_{12}$ and ESC$_{3}$) and open-field ambulation. Freezing showed a strongly negative loading on this dimension too. This factor reflects a strategy of the defense: active escape versus passive freezing. Because freezing may share a state of excessive fear and stress, it was called Fear Avoidance.

Freezing, thus, correlated with both factors. This provides additional evidence that this behavior pattern may reflect fear and stress, as well as unwillingness to explore, relaxed state, and lack of arousal (Gerlai & Csányi, 1990; Gerlai & Hogan, 1992). The second principal-components analysis is also consistent with this (see below).

Table 5 shows the results of a series of Cox proportional hazard regression analyses. All three models were statistically significant as determined by chi-square test. For each exposure, the first principal component—Activity Explora-

Table 5
Relationships Between the Latency to Enter the Inspection Compartment in Different Test Exposures and the Principal Components

Principal component	β	SE	t	χ^2 (3)
First test exposure				18.83**
Activity Exploration	1.410	0.365	3.86[a]	
Fear Avoidance	0.455	0.347	1.31	
Second test exposure				18.54**
Activity Exploration	1.653	0.491	3.36[a]	
Fear Avoidance	0.679	0.390	1.74	
Third test exposure				10.15*
Activity Exploration	1.125	0.406	2.77[a]	
Fear Avoidance	0.569	0.378	1.51	

Note. Betas are the regression weights. $N = 29$ for all chi-square tests.
[a]Only the predictors with $|t| = |\beta/SE| > 2$ were considered significant.
*$p < .01$. **$p < .001$.

tion—was thoroughly associated with a greater hazard (beta weights positive; see Table 5) and therefore with a shorter latency to enter the inspection compartment. The second principal component—Fear Avoidance—tended to show a similar pattern, although in a much smaller degree, which was judged nonsignificant. Thus, the latency to explore a novel compartment correlated highly with other exploratory measures but not with fear and escape.

The results of the second component analysis are presented in Table 6. Three principal components with the eigenvalues greater than unity together explained 77% of variance. The Cattell's scree test, however, seem to indicate only one factor. But the varimax-rotated factor pattern matrices for this range of solutions appeared quite similar. The variables that loaded on the third factor correlated weakly with both of the first two factors in both rotations. I decided therefore to base the decision about the number of factors to extract on Kaiser's criterion. The third factor, however, while explaining 13% of variance, was determined by variables that were not significantly correlated. I left it uninterpreted. This third factor, in addition, did not appear in the accompanying factor analysis (the decision about the number of factors was based on the Root 1 and the VSS tests as described above). No one residual correlation exceeded .19 (the maximum value acceptable with $N = 28$), indicating that the component solution was satisfactory.

A clear pattern emerged for the first two principal components (see Table 6). The first one was loaded most by the locomotor measures—positively by moving and STOP, but negatively by freezing. It was called Locomotion. The second component was loaded positively by freezing plus negatively by $\mathrm{LOOK}_{\mathrm{M}}$, as well as by the tendencies to establish contacts with schooling conspecifics and the mirror image. This factor was called (inverse) Sociability.

Step 3: Canonical correlation analysis. Eight behavioral measures were subjected to the canonical correlation analysis. The first domain of variables represented the individual scores on the first two principal components based on the variables obtained in the open-field and inspection tests—Activity Exploration and Fear Avoidance,—whereas the second domain encompassed the following variables: $\mathrm{FRZ}_{\mathrm{M}}$, $\mathrm{MOVE}_{\mathrm{M}}$, $\mathrm{LOOK}_{\mathrm{M}}$, $\mathrm{MIRR}_{\mathrm{M}}$, $\mathrm{FRZ}_{\mathrm{S}}$, and $\mathrm{ATMPT}_{\mathrm{S}}$, which showed largest correlations with the components.

The dimensionality test showed that two canonical variates were necessary to represent relationships between these domains of variables (Table 7). The canonical loadings for the two domains of variables studied are presented in Table 7. As expected, each principal component turned out to be closely correlated with only one particular canonical variate and loaded only negligibly on the other. This indicates that

Table 6
Varimax-Rotated Component Loadings: Schooling and Mirror Tests Variables

Variable	Locomotion	Sociability	Not interpreted
Schooling test			
$\mathrm{FRZ}_{\mathrm{S}}$	−.67[a]	.64[a]	−.11
$\mathrm{STOP}_{\mathrm{S}}$	.89[a]	.10	−.04
$\mathrm{MOVE}_{\mathrm{S}}$	.86[a]	−.20	.06
$\mathrm{ESC}_{\mathrm{S}}$	−.11	−.33	.81[a]
$\mathrm{ATMPT}_{\mathrm{S}}$	.13	−.89[a]	−.09
Mirror test			
$\mathrm{FRZ}_{\mathrm{M}}$	−.60[a]	.67[a]	−.33
$\mathrm{STOP}_{\mathrm{M}}$	.72[a]	−.13	.49[a]
$\mathrm{MOVE}_{\mathrm{M}}$	.72[a]	−.43	−.04
$\mathrm{ESC}_{\mathrm{M}}$	.20	.24	.79[a]
$\mathrm{LOOK}_{\mathrm{M}}$	.23	−.76[a]	.18
$\mathrm{MIRR}_{\mathrm{M}}$	.01	−.80[a]	−.03
Eigenvalue	5.12	1.90	1.43
Variance accounted (%)	46.55	17.30	13.03

Note. See text for full definitions of behaviors.
[a]Interpretable loadings.

Table 7
Canonical Analysis of the Relationships Between the Principal Components Based on the Open-Field and Inspection Tests Versus Mirror Test Variables: Canonical Loadings

Variable	Fear Avoidance	Approach
First domain		
Activity Exploration	−.07	−.998[a]
Fear Avoidance	.999[a]	−.04
Second domain		
$\mathrm{FRZ}_{\mathrm{S}}$	−.40	.63[a]
$\mathrm{ATMPT}_{\mathrm{S}}$	.23	−.64[a]
$\mathrm{FRZ}_{\mathrm{M}}$	−.44	.69[a]
$\mathrm{MOVE}_{\mathrm{M}}$	.38	−.67[a]
$\mathrm{LOOK}_{\mathrm{M}}$	.12	−.90[a]
$\mathrm{MIRR}_{\mathrm{M}}$	.76[a]	−.28
Canonical R	.84	.66
χ^2 (df)	39.75 (12)	12.81 (5)
p	<.0001	.025

Note. See text for full definitions of behaviors.
[a]Interpretable loadings.

the components really represented univocal behavioral dimensions.

The first canonical variate was loaded positively by the second principal component (Fear Avoidance) and attempts to contact with the mirror image ($\mathrm{MIRR_M}$). To the extent the tendency to contact with the mirror reflected aggressiveness (e.g., Franck & Ribowski, 1987), this relationship may illustrate the often-found positive correlation between boldness and aggressiveness (Archer, 1988). There were also low (about .4) negative loadings by freezing (both $\mathrm{FRZ_S}$ and $\mathrm{FRZ_M}$), implying that the fish were not much stressed in the presence of conspecifics. The second variate correlated closely with the first principal component (Activity Exploration). It was also heavily loaded by the social tendency measures ($\mathrm{ATMPT_S}$ and $\mathrm{LOOK_M}$), locomotion during the mirror test ($\mathrm{MOVE_M}$), and freezing ($\mathrm{FRZ_S}$ and $\mathrm{FRZ_M}$). This dimension represents the tendencies to express exploratory and schooling tendencies. I called it Approach.

Analysis of Discontinuous Variation

Discontinuous variation. The distribution of the percentage of time spent freezing during the first subtest of the inspection test (i.e., a confined novel environment) deviated from normal (Shapiro-Wilk's test: $W = 0.73$, $p < .0001$). Two modes appeared: Certain guppies froze either much of the time or, alternatively, only a very short time (see Figure 2). But the distribution was bimodal rather than truly discontinuous because 3 fish occupied an intermediate position (approximately 50% to 70%) on the freezing axis. Thus, the whole continuum was split into two alternative strategies: "freezers" and "nonfreezers." To reduce the possibility of behavior suppression in the subsequent dimensional analysis, I attached the intermediate fish arbitrarily to the freezers group, which led to a slightly more conservative cutoff point score equal to 40%. Similar bimodal patterns of the distributions were observed in most other exposures (Shapiro-Wilk's test: $ps < .001$), and as a result of high intercorrelations (see above), these must be relatively stable. Furthermore, the cluster analysis of nine freezing scores (inspection test: 3 subtests × 3 test exposures) revealed a clear underlying structure consisting of two distinct clusters (see Figure 2). There were only 4 guppies that switched from low to high freezing with repeated test exposures, which might simply indicate habituation of curiosity.

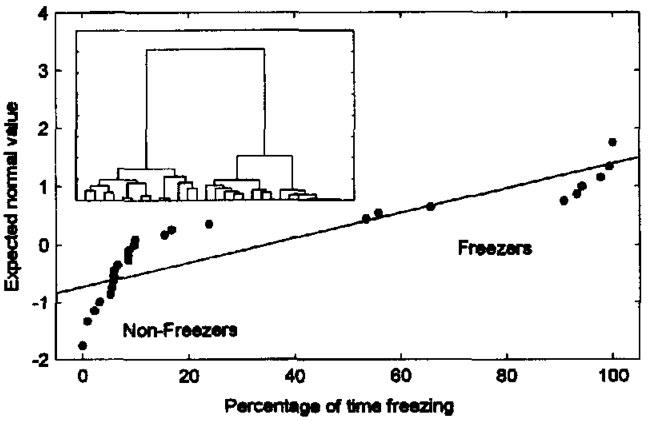

Figure 2. Normal probability plot for the percentage of time spent freezing during the first subtest of the inspection test (a confined novel environment). The results of cluster analysis involving nine standardized freezing scores are also shown. Two distinct clusters are apparent in the cluster tree.

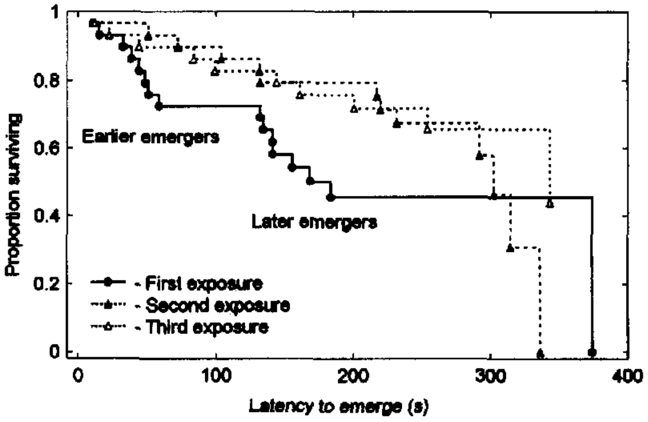

Figure 3. Survivorship plot function for the tendency to emerge in an adjacent novel compartment during the first, second, and third exposures of the inspection test. It shows the proportion of guppies not emerging ("surviving") up to the respective time interval.

Likewise, the survival curve for the tendency to enter an adjacent novel compartment (which shows the proportion of guppies not entering up to a particular time) during the first exposure of the inspection test (see Figure 3) indicated that the overall distribution differed from exponential, characterized by a constant hazard rate ($\lambda \pm SE = .0035 \pm .0013$); $\chi^2(5, N = 29) = 15.70$, $p = .008$. In this case, two distinct strategies may be observed: emerging in an adjacent novel compartment, first, with a short latency, and, second, after some delay (approximately 130 s). Only nonfreezers belonged to the former group ($n = 8$), whereas the latter group of late emergers consisted of 10 (48%) freezers and 11 (52%) nonfreezers.

During the second exposure, there was no evident discontinuous variation in the latency to enter the novel arena (see Figure 3), although the distribution significantly deviated from exponential ($\lambda \pm SE = .0027 \pm .0009$); $\chi^2(4, N = 29) = 11.35$, $p = .022$. However, during the third administration of the same behavioral test, the corresponding latency proved to be exponentially distributed ($\lambda \pm SE = .0023 \pm .0011$); $\chi^2(5, N = 29) = 3.08$, $p = .688$, *ns* (see Figure 3). This pattern means that, despite initial discontinuous variation and close intertrial correlations (see the reliability analysis), with habituation the fish tended to enter in an overtly random fashion (like radioactive decay), suggesting a decline of curiosity: The probability to make a decision to enter the novel area (i.e., hazard rate in terms of survival analysis) was independent of the time elapsed since access was allowed.

Table 8

Varimax-Rotated Component Loadings: Open-Field and Inspection Test Variables

Variable	Approach	Fear Avoidance
Open-field test		
$\mathrm{AMB}_{\mathrm{OF}}$	.31	.62[a]
Inspection test		
FRZ_{12}	−.58[a]	−.69[a]
MOVE_{12}	.87[a]	.06
ESC_{12}	−.36	.83[a]
FRZ_{3}	−.71[a]	−.61[a]
MOVE_{3}	.77[a]	−.04
ESC_{3}	−.25	.91[a]
$\mathrm{INSP}_{\mathrm{max}}$	.82[a]	−.18
Eigenvalue	3.40	2.55
Variance accounted (%)	42.52	31.89

Note. See text for full definitions of behaviors.
[a] Interpretable loadings.

Principal-components analysis and canonical analysis. Two principal components appeared (see Table 8) with eigenvalues greater than unity, which explained 74% of the total variance. Both were virtually identical with those extracted in the complete sample (Activity Exploration and Fear Avoidance).

The results of the canonical correlation analysis turned out also exactly the same. The chi-square test for the dimensionality of the relationships between the components and the schooling and mirror tests variables indicated that two dimensions were necessary (see Table 9). The pattern of canonical loadings for the two sets of variables is similar to that observed in the complete sample (Table 9).

Sequential Sampling Bias

The first principal component, Activity Exploration, turned out to show a modest, albeit significant, correlation with the capture order ($\rho = -.40$, $N = 29$, $p = .032$). However, the second factor, Fear Avoidance, proved to be uncorrelated with it ($\rho = .12$, $N = 29$, $p = .55$, *ns*). All individual behavioral indexes, on which these principal components were based (i.e., which had high loadings on these factors) showed the same patterns. For example, locomotion in a confined novel environment (MOVE_{12}, which loaded primarily on the Activity Exploration; see earlier), was closely correlated with the capture order ($\rho = -.61$, $N = 29$, $p < .001$). However, open-field ambulation ($\mathrm{AMB}_{\mathrm{OF}}$), an amalgam of both dimensions, turned out to be independent of the capture order ($\rho = -.12$, $N = 29$, $p = .53$). An analysis of the latencies to explore a novel area also revealed a nonrandom pattern ($\rho = -.42$, $N = 29$, $p = .024$), with the first fish captured being the earlier emergers.

Table 9

Canonical Analysis of the Relationships Between the Principal Components Versus Schooling and Mirror Test Variables: Canonical Loadings

Variable	Fear Avoidance	Approach
First domain		
Activity Exploration	−.03	−.9996[a]
Fear Avoidance	1.00[a]	.00
Second domain		
$\mathrm{FRZ}_{\mathrm{S}}$	−.42	.51[a]
$\mathrm{ATMPT}_{\mathrm{S}}$	.34	−.56[a]
$\mathrm{FRZ}_{\mathrm{M}}$	−.50[a]	.54[a]
$\mathrm{MOVE}_{\mathrm{M}}$	.33	−.31
$\mathrm{LOOK}_{\mathrm{M}}$	.34	−.89[a]
$\mathrm{MIRR}_{\mathrm{M}}$	.79[a]	−.12
Canonical *R*	.88	.79
χ^2 (*df*)	30.76 (12)	12.25 (5)
p	.002	.032

Note. See text for full definitions of behaviors.
[a] Interpretable loadings.

Discussion

Taken together, the results of the present study suggest that individual behavioral differences in guppies are worth considering on several levels. On the lowest level, one can find specific responses, acts, and so on. But on the higher level, broader "personality" dimensions appear, which are inferred from observed covariations between different tests and measures. This finding is in good agreement with some general theories postulating hierarchical organization of the properties of the behavioral phenotype (see Royce & Mos, 1979).

The first step of the data analysis revealed relatively high consistencies of most behavior measures. At the second step, two independent dimensions appeared in the first domain of situations that involved novelty and a predator: Activity Exploration and Fear Avoidance. In addition, in the schooling and mirror test domain, two uncorrelated factors appeared: Locomotion and Sociability. The third stage of the data analysis revealed the existence of even higher order dimensions. In this way, Activity Exploration correlated with the schooling tendencies, which implies a broader factor, called Approach. The Fear Avoidance factor correlated with the tendency to respond to the mirror image, also implying the existence of a broader personality dimension.

Finally, it was shown that the Activity Exploration (but not the Fear Avoidance) factor interacted with the sampling procedure, so that the most exploratory guppies were captured first (see also Lecci, Borshini, Volterra, & Meli, 1990, for an example of sequential bias in emotionality in mice). Presumably, the catching net was initially perceived by naive guppies as a novel object, and the most exploratory fish approached to explore it. This not only emphasizes the need to pay close attention to randomization of subjects in research (as the personality is really general and may translate to various situations), but also further highlights consistency and generality of this dimension of personality.

Although I did not explicitly assess how stable particular behavioral measures in the guppy are (the consistency was studied over a short period in the nonsocial tests and 2 weeks in the social tests), the behavioral traits were predictable across many situations separated by months (as each between-tests period was approximately 1 month). Thus, the behavioral traits in the guppy are, in fact, consistent over time. Many behavioral traits in fish may be fairly consistent over time (e.g., Francis, 1990, demonstrated longitudinal stability of aggressiveness in a cichlid fish).

The present investigation not only documents consistent individual differences but also reveals a structure of higher order personality dimensions that are similar to the dimensions observed in diverse species: active and sociable versus passive (Approach), and bold versus fearful (Fear Avoidance).

There are many similarities between the personality structures across several vertebrate species, including humans, implying an involvement of common physiological or adaptive mechanisms: Similar two-dimensional patterns appeared, with the dimensions closely resembling Approach (activity, curiosity, sensation-seeking, and sociability) and Fear Avoidance (emotionality, shyness, and autonomic responsiveness; Budaev, 1996; Eysenck & Eysenck, 1985; Garcia-Sevilla, 1984; Royce, 1977). In this way, it is tempting to suppose (e.g., Budaev, 1996; Eysenck & Eysenck, 1985) that in humans the dimensions analogous to Approach and Fear Avoidance represent two major personality dimensions: Extraversion–Introversion and Neuroticism, which are known to have the largest replicability, clear physiological background, and high heritability. Further studies are needed to ascertain, for example, whether the same neurotransmitter systems mediate these dimensions in a similar way in a wide range of species (Zuckerman, 1994).

Fear Avoidance Personality Dimension

The Fear Avoidance factor probably represents a motivational system governing the responses of fish to aversive stimuli. Consequently, this system may be thought to evoke fear, an emotional and motivational state normally induced by exposures to potentially dangerous objects or situations (Boissy, 1995; Brain, 1990).

Although some investigators (e.g., Archer, 1979) argue against the unitary concept of fear because various behaviors indicating it often correlate poorly, other ethologists (e.g., Boissy, 1995; Russell, 1979) overcome the problem by postulating that fear responses are stimulus specific and thereby adaptive to particular situations. Moreover, there exists sound evidence that various fear-indicating behaviors are not independent (Jones, Mills, & Faure, 1991) and really reflect a single general motivational construct.

Approach Personality Dimension

Because the measures of exploratory behavior correlated closely with the schooling tendency, determining a single dimension is important, because this emphasizes the similarity with Extraversion and indicates that both exploratory and social behavior may be governed by common controlling factors. Yet, the locomotion of guppies in the open-field and inspection tests might reflect a tendency to reinstate contact with conspecifics (see Gallup & Suarez, 1980; Suarez & Gallup, 1983, for more discussion), not only exploration. However, this is unlikely. First, predator inspection, an exploratory behavior functionally unrelated to the searching for conspecifics, proved to be moderately correlated with both schooling tendency measures (with $\mathrm{ATMPT_S}$ $r = .43$, $N = 28$, $p = .023$ and $\mathrm{LOOK_M}$ $r = .68$, $N = 28$, $p < .001$). Second, I found no one significant correlation (all correlations were smaller than .2 with $p > .3$) between the inspection test escape and either schooling tendency measure ($\mathrm{ATMPT_S}$ or $\mathrm{LOOK_M}$), implying that the escape behavior was also unrelated to it. Another alternative is that the extreme freezing observed in some subjects may suppress all other behavior, causing, in turn, spurious correlations. But this is also unlikely because, as a separate analysis showed, even in the low-freezing subjects the same patterns of correlations emerged.

Hence, there is not much reason to suggest hidden independence of the social and exploratory tendencies. The hypothesis of common underlying factors is much more plausible, although it needs further testing (e.g., by genetic selection and physiological manipulation). However, with this relationship it would be fundamentally impossible to separate two different interpretations of this component of open-field behavior; namely, the more traditional view based on exploration and curiosity (Walsh & Cummins, 1976) and that involving social reinstatement (Suarez & Gallup, 1983).

Is Personality Continuous?

The findings suggest that there exists a bimodal, though not completely discontinuous, pattern of individual variation in two important aspects of guppy behavior: the tendency to freeze in a confined novel environment and the latency to commence exploration of a novel environment. However, this bimodality did not represent a single personality dimension and must be viewed as an amalgam of both Activity Exploration and Fear Avoidance. Similar results are observed in humans: Alternative styles of coping with stress (e.g., Type A and Type B behavior), while often easily separable (e.g., Lazarus & Folkman, 1984), nonetheless do not represent a unifactorial personality trait. Behavioral inhibition in stressful situations could also be associated with various personality traits: high fearfulness, low extraversion, or both (Asendorpf, 1993; Cheek & Briggs, 1990).

The strategies found in the present study probably represent alternative styles of coping with stress and challenge, analogous to those described in mammals (see Benus et al., 1991, for a review) as well as in birds (Verbeek, Drent, & Wiepkema, 1994). In these species, alternative strategists differed in many aspects of behavior, including aggression (offense and defense), shuttlebox avoidance conditioning, responses to inescapable shock, and environmental changes. Active copers tended to manipulate the environment, whereas passive copers adjusted their own behavior to the environmental demands. From this viewpoint, it would be informative to study the behavior of alternative strategists in a known environment, to see if active copers show a routinized activity and diminished attention to subtle environmental changes (Benus et al., 1991).

These bimodal patterns, together with the finding that the latencies to enter a novel compartment tend to be more randomized with habituation, may illustrate an interesting phenomenon, namely that consistent individual differences become pronounced in situations of mild stress (e.g., Alados, Escos, & Emlen, 1996; Gerlai & Csányi, 1990; Suomi, 1983). For example, heritability estimates for ambulation and defecation in rats decrease with repeated exposures of the open-field test (Broadhurst & Jinks, 1966). Similarly, in the paradise fish (*Macropodus opercularis*), different genotypes tended to behave more differently in novel situations than in the home tank (Gerlai & Csányi, 1990). Thus, randomized behavioral components tend to be particularly pronounced in nonthreatening situations and could mask possibly consistent individual differences.

There is an evidence from field studies of salmonid fish that, under the same environmental conditions, there are alternative active and passive behavioral strategies, for example, foraging movement patterns (Biro & Ridgway, 1995; McLaughlin et al., 1992). Also, profound and relatively clear-cut differences in the boldness in a novel environment were recently found in the European wrasse (*Symphodus ocellatus;* Budaev, 1997), and these differences were associated with other salient behavioral strategies: schooling tendency, general activity, and habitat preference. Thus, the alternative coping styles in fish may translate to many other situations and therefore are likely to be ecologically important (see also Wilson, Coleman, Clark, & Biederman, 1993, for ecological implications of shyness–boldness in a sunfish). For example, Ketterson and Nolan (1992) suggested that animals that are active in challenging situations would play the territorial mating strategies whereas passive and fearful animals would tend to attempt to sneak fertilization.

Evolutionary Implications of Personality

Probably in most cases the existence of a phenotypic correlation would suggest, not necessarily however, that a genetic correlation could be present (reviewed by Cheverud, 1988; also see Bakker, 1994). The available data suggest that the two basic dimensions discovered in this study coincide with the gross pattern of adaptive between-populations variation in the guppy in Trinidad, which is largely heritable (see Magurran et al., 1992, for a review of heritable interpopulation differences). In particular, the fish sympatric with predators are characterized by a whole array of fear-indicating behaviors and higher schooling, whereas allopatric fish show pronounced aggressiveness and are not much afraid of predators (see Magurran, 1993; Magurran et al., 1992, for reviews). Yet, the fish sympatric with predators typically emit higher levels of predator inspection, and predator harassment is extremely risky (Dugatkin & Godin, 1992; Magurran & Seghers, 1990). This poses a problem on the possible unidimensional shyness–boldness continuum (conceived as a propensity to take risks; see Wilson et al., 1993, 1994) in that the same fish may exhibit both "shy" and "bold" behavior patterns. Obviously, two distinct dimensions must be involved, and in the context of the present study the guppies from heavily predated populations would be characterized by high approach tendency and high fearfulness. Thus, common causal factors determining across-domain and, presumably, genetic covariations may impose constraints on the evolutionary processes; for example, evolution could proceed rapidly in some directions but be extremely slow in other ones (Arnold, 1992; Bakker, 1994; Price & Langen, 1992). No single character may be ideally analyzed for its adaptive significance without regard to other ones that an organism possesses (Dobzhansky, 1956). Thus, the dimensions of personality are necessary to take into account when one considers mechanisms of behavior evolution. All this suggests that personality should be viewed as a useful unifying framework integrating comparative, causal, and proximate approaches to the study of individual behavioral differences.

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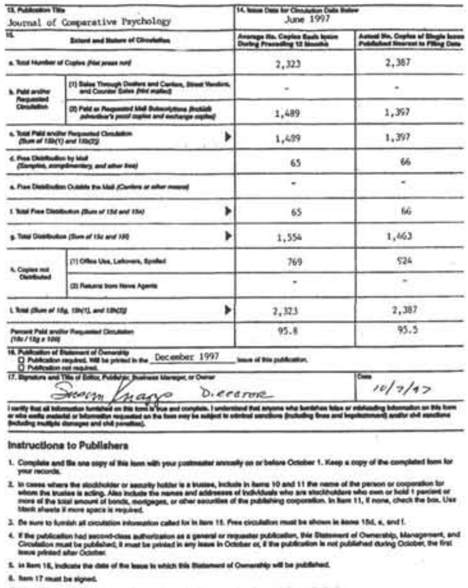

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