Individual differences in parental care and behaviour profile in the convict cichlid: a correlation study

SERGEY V. BUDAEV, DMITRY D. ZWORYKIN & ANDREI D. MOCHEK

A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences

We examined whether individual differences in patterns of parental care relate to individual differences in situations involving novelty, risk and aggression in the convict cichlid, *Cichlasoma (Archocentrus) nigrofasciatum*. Individual differences in situations of novelty and risk could be summarized along two axes: Freezing versus Activity and Activity-Inspection versus Freezing. However, these factors were not independent and formed a single higher-order dimension of general activity. Parental locomotor activity was negatively correlated with the Freezing versus Activity factor in females. Males that did little brood provisioning tended to be less active in the presence of a novel fish. Individuals that spent more time near their offspring at late brood stages were less inhibited in behavioural tests. Furthermore, extreme assortative mating by body size was found ($r_S=0.91$). The cichlids also spawned assortatively by the factor Freezing versus Activity and by the general activity factor ($r_S \geq 0.49$), but not by the factor Activity-Inspection versus Freezing or by aggressiveness.

© 1999 The Association for the Study of Animal Behaviour

Individual differences in behaviour, found in virtually all species, may be maintained within a population through natural selection and could therefore be adaptive (Slater 1981; Clark & Ehlinger 1987; Magurran 1993; Wilson et al. 1994). Recent investigations (e.g. Stevenson-Hinde 1983; Clark & Ehlinger 1987; Francis 1990; Benus et al. 1991; Mather & Anderson 1993; Wilson et al. 1993, 1994; Budaev 1997; Gosling 1998) have emphasized the importance of studying temperament traits that are consistent over time and across situations, because such stability suggests the involvement of stable physiological, motivational, cognitive and adaptive mechanisms and implies some degree of heritability. However, few studies have analysed how individual differences in one situation relate to those in other situations and what their ecological consequences may be (but see Wilson et al. 1993; Budaev 1997; Budaev & Zhuikov 1998; Coleman & Wilson 1998).

In this study we analysed whether individual differences in patterns of parental care are related to individual differences in situations involving novelty, risk and aggression in the convict cichlid, *Cichlasoma (Archocentrus) nigrofasciatum*. These behavioural categories may involve interactions between various motivational systems, such as fear, exploration and aggression, and are potentially important in the adaptive sense. Individual differences in at least some of them are known to be consistent (Stevenson-Hinde 1983; Francis 1990; Benus et al. 1991; Wilson et al. 1993; Budaev 1997). Because parental care is a costly component of reproduction, individual differences in it may have important evolutionary implications (Clutton-Brock 1991). Individual differences in patterns of parental behaviour have already been documented in cichlids (e.g. Zworykin et al. 1998). Furthermore, temperament dispositions affect mothering style in rhesus monkeys, *Macaca mulatta* (Maestripieri 1993), and mouse, *Mus musculus*, strains with alternative styles of coping with stress and challenge differ in their maternal behaviour (Benus & Röndigs 1996).

METHODS

Subjects and Maintenance

The convict cichlid is a biparental, substrate-brooding species inhabiting Central American streams and lakes. Our stock was descended from fish obtained from a private aquarium breeder. Twenty-three pairs (standard length 59–76 mm in males, 43–66 mm in females) were used in the study (total $N=46$). The photoperiod was a 10:14 h light:dark cycle. Water temperature was maintained at $26 \pm 1°C$. Both adults and fry were fed with commercial dry flakes (0.7–0.9 g of food per pair with brood) five times per week.

Correspondence: S. V. Budaev, A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospect 33, Moscow 117071, Russia (email: irene@irene.msk.ru).

Prior to experiments (from the fry period), all fish were maintained in a large tank (1.49 × 1.37 m and 0.74 m high, water depth 0.6 m), containing about 80 same-age conspecifics (with the sex ratio close to 1:1), where they were allowed to choose their mates freely. The large maintenance tank contained several large stones and caves (sections of clay flowerpots), as well as a single, removable, dark-brown spawning box (15 × 8 × 9 cm) with a guillotine door. The fish were allowed to form pairs freely and take up the caves and the box. When we saw that the spawning box was occupied by a cichlid pair and both individuals happened to be inside, we closed the door and quickly moved the box to an individual breeding aquarium. Each breeding aquarium (50-litre volume, 46 × 28 × 39 cm) contained half a clay flowerpot as a potential spawning substrate and about 3 cm of natural gravel. Each pair was maintained there for the whole experiment.

All pairs were categorized as 'spawning' or 'nonspawning', depending on whether they spawned within the next month. Spawning pairs (N=13) were allowed to rear their offspring. One month after parental care ceased, we tested the fish in several behavioural tests to ascertain their behavioural profiles. The nonspawning pairs (N=10) were maintained in individual breeding aquaria for 1 month, after which they were also tested in the same tests. Measurements of parental behaviour and behavioural profiles were conducted blind to each other.

Parental Behaviour

As in previous studies (e.g. Wisenden et al. 1995; Zworykin 1998; Zworykin et al. 1998), the brood development was classified into five stages: egg; wriggler; 3 days as fry; 10 days as fry; 17 days as fry. We scored three behavioural variables once at each brood stage: the frequency (number per 10-min period) of parental fin digging (a kind of parental food-provisioning behaviour, see Wisenden et al. 1995); locomotion (the percentage of time the parent moved further than one body length in any direction); and the percentage of time spent near the brood (within one body length of the parent). Recording sessions were carried out between 1100 and 1400 hours, before the fish were fed, and each observation, one per brood stage, lasted 10 min. Only one brood cycle was observed per breeding pair. The observer recorded the behaviour of the fish as spoken comments on audiotape. We used an event-recording software package to analyse the tapes (Budaev 1995).

Behavioural Profiles

All parents were tested in three tests as described below with 1 week between tests. In each test, subjects were selected in a randomized order to prevent sequential artefacts and were not fed prior to testing. Observations took place between 1300 and 1600 hours. They were conducted through a small window in a screen separating the experimental apparatus from the observer to avoid disturbing the fish. We tried to make experimental
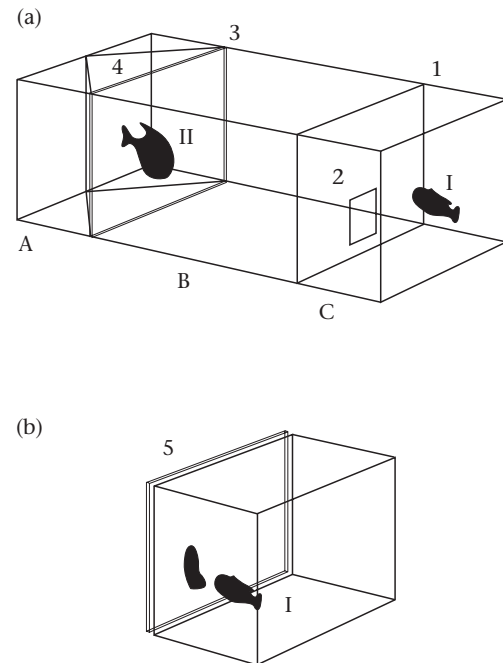

Figure 1. Apparatus used for (a) the novel fish test and (b) the mirror test. The tank consisted of novel fish (A), inspection (B) and home (C) compartments. 1: Opaque partition; 2: sliding door; 3: glass partition; 4: V-like folds; 5: mirror. I: Test fish; II: novel fish.

conditions identical for all fish. Not more than six individuals were tested on any one day. The percentages of time spent displaying various behaviours were recorded on audiotape. Previous studies indicated that behavioural traits measured in such tests may be consistent over time and across situations (Budaev 1997).

Open field test

This test was conducted in a hexagonal tank 0.9 m in diameter, with the water level at 8 cm. Initially an individual was gently released into a white bottomless opaque plastic cylinder (start box, placed in the centre of the tank) for 5 min to ensure that it acclimated after the handling. After that, the cylinder was lifted and the behaviour of the fish was observed from above for 5 min. We recorded on audiotape the time spent freezing and moving in the open field.

Novel fish test

The novel fish test was done in an aquarium (60 × 30 × 20 cm, water depth 15 cm) with three compartments (Fig. 1a). 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 third compartment, containing a novel fish (angelfish, *Pterophyllum scalare*, standard length 60 mm), was located behind a transparent glass wall. It also contained a white V-like plastic fold, preventing the angelfish from hiding in a corner.

Before the test, we gently transferred a cichlid to the start box placed in the centre of the home compartment with the door closed. The fish was given 5 min to recover

from capture and transfer, the box was raised and the behaviour of the fish was observed for 5 min (first recording session). The door was then opened and, as soon as the individual entered the inspection compartment, the second recording session began, and continued for 5 min. If the subject did not enter within 7–8 min (15 fish; entrance was not related to sex or spawning group; Fisher's exact test: Ps>0.53), we placed it in the same start box for 5 min, but this time within the inspection compartment, about 5 cm from the door.

In both test sessions we recorded on audiotape freezing, movements and escape attempts (when the fish tried to go through the glass walls of the open field). During the second session, we also recorded the percentage of time the fish spent inspecting the novel fish. Inspections were defined as apparent approaches to the novel fish followed by more-or-less prolonged visual fixations on it. We also recorded the latency to enter the inspection compartment as well as the latency to approach the novel fish.

Mirror test

The mirror test was done in an aquarium measuring $17 \times 30 \times 20$ cm with a mirror (30×20 cm) attached to its one wall (Fig. 1b). A sheet of a semiopaque plastic film was placed in front of the mirror. It could be slid away by pulling an attached cord. In preliminary observations, the fish did not show any aggressive behaviour when the mirror was covered by the film.

First, an individual was gently released into the test apparatus when the mirror was covered with the semiopaque film. After 10 min allowed for exploration and adaptation, the film was pulled away. As soon as the fish performed any aggressive behaviour towards its image, we started the recording session, continuing for 6 min. As in the previous test, we recorded on audiotape freezing, movements and escape attempts. Also, we recorded the percentage of time devoted to aggressive displays and bites directed to the mirror image, as well as the latency to the first interaction with the mirror. All individuals approached and interacted with their mirror images.

Ethical Note

These behavioural tests involved minimal stress to the subjects. There were some signs of stress in the fish, such as freezing, especially in the open field test, but this had no adverse effects. Stress was also minimized by the use of the start box for acclimation after the capture and transfer handling. The angelfish was separated from the convict cichlid by a glass partition and no physical contact was possible.

Statistical Analysis

Nonparametric and parametric statistical methods were used, whenever appropriate. The Krauth (1988) extension of the Spearman correlation test was used for censored latency data. As we had small sample sizes ($N=10$ and 13), we computed 95% confidence regions (Brown &

Benedetti 1977) and exact P values based on Monte Carlo estimation for Spearman correlation coefficients. The P values were two tailed in most cases. However, in the analysis of assortative mating, we used one-tailed tests because positive relationships were expected while negative ones could not be easily interpreted and were conceptually equivalent to nonsignificant results (Kimmel 1957). Furthermore, computation of confidence regions for correlation coefficients showed that negative values were extremely unlikely when significant assortment was observed.

This study represents an exploratory correlational analysis rather than tests of specific hypotheses, in which significance in any individual test would lead to the rejection of the hypothesis. The statistical tests were often not independent, making existing adjustment techniques too conservative (Wright 1992). It was also difficult to establish which were the appropriate families of tests (that is, collections of tests addressing common hypotheses); owing to the large number of relationships analysed, treating all the tests as a single family would have greatly reduced statistical power (see Chandler 1995). Consequently, the possibility of type I error inflation was not taken into account and we did not adjust the P values.

We calculated Cronbach alpha reliability coefficients (Wherry 1984) to assess the consistency of particular behavioural measures. In factor analysis, we used the MINRES algorithm (in which the initial estimates of factor loadings are adjusted iteratively to minimize the residual sum of squares) for factor extraction. Normalized Varimax, Promax (power=4) and direct Oblimin (gamma=0.0), as well as the Wherry hierarchical method of factor rotations were applied (Wherry 1984). To estimate the number of factors to extract, we used the Kaiser's eigenvalue-one rule, the scree test and the parallel analysis of random simulated data (Zwick & Velicer 1986), involving 100 random samples in each case.

RESULTS

Individual Differences in Parental Behaviour

Individual differences in parental brood provisioning (the frequency of fin digging) were highly consistent over the five brood stages (Cronbach alpha=0.92), with females being somewhat more stable (alpha=0.90) than males (alpha=0.83). Similarly, the percentage of time for which the parents moved was moderately consistent (Cronbach alpha=0.78 overall; 0.77 in males and 0.78 in females). This allowed us to aggregate these measures over the five brood stages into the respective composite scores, which yielded the composite brood-provisioning score and the composite parental locomotion score. These scores did not correlate significantly, however (P>0.2 in both sexes). There were significant correlations between males and females within pairs in the aggregated brood-provisioning score (r_S=0.59, 95% confidence region 0.20–1.00, N=13, P=0.031) and aggregated activity score (r_S=0.88, 95% confidence region 0.75–1.00, N=13,

Table 1. Factor analysis of behavioural measures obtained in the behavioural tests

	Varimax rotation		Wherry rotation
	Factor 1	Factor 2	General factor
Open field freezing	0.51‡	−0.05	−0.33
Freezing*	0.97‡	−0.24	−0.71‡
Moving*	−0.85‡	0.11	0.56‡
Escape*	−0.59‡	0.29	0.52‡
Freezing*	0.29	−0.95‡	−0.73‡
Moving†	−0.41‡	0.71‡	0.66‡
Escape†	−0.40‡	0.56‡	0.56‡
Novel fish inspection†	0.10	0.74‡	0.37

Factors 1 and 2 were interpreted as Freezing versus Activity and Activity-Inspection versus Freezing, respectively.
*First recording session of the novel fish test.
†Second recording session of the novel fish test (inspecting the novel fish).
‡Interpretable factor loadings (≥0.4).

$P=0.0002$). That is, the parents within a pair behaved similarly.

Because the percentage of time spent near the brood had a significantly skewed distribution and there were outliers, the original values were rank transformed prior to the consistency analysis. This behavioural measure was weakly stable (Cronbach alpha=0.66). In addition, whereas in females the alpha coefficient reached a moderate value of 0.52, individual differences proved to be unstable in males (Cronbach alpha=0.27). Consequently, data aggregation was not appropriate. The male–female correlations in this behaviour approached significance only when the fry were 3 days old ($r_S=0.67$, 95% confidence region 0.29–1.00, $N=13$, $P=0.016$) and 17 days old ($r_S=0.55$, 95% confidence region 0.09–1.00, $N=13$, $P=0.051$).

Behavioural Dimensions

Eight behavioural variables (see Table 1) scored in the open field and inspection tests were subjected to factor analysis. They were rank transformed prior to analysis to stabilize the correlation matrix. Rank transformation converts the Pearson correlation coefficients into Spearman correlations, and the latter are more appropriate for factor analysis in some cases (see Atkinson 1988 for more discussion). Measures of sampling adequacy (Dziuban & Shirkey 1974) indicated that the correlation matrix was appropriate for factor analysis (Kaiser–Meyer–Olkin measure of sampling adequacy=0.68; Bartlett's sphericity test: $\chi^2_{28}=263.37$, $P<0.0001$).

All three criteria (root-one, scree test and parallel analysis) agreed that two factors should be extracted. They explained 64% of the total variance. Table 1 shows the orthogonal Varimax-rotated factor loadings. The first factor was primarily associated with activity versus freezing in the open field test, in the first recording session of the inspection test (in the absence of the novel fish) and, to a lesser degree, in the presence of the novel fish. The

second factor had primary loadings by freezing versus activity and inspection during the second recording session of the novel fish test, when the subject was confronted with a strange fish. Accordingly, these behavioural dimensions were tentatively interpreted as Freezing versus Activity and Activity-Inspection versus Freezing. In oblique rotations, however, the factors were inversely correlated (interfactor correlations were −0.47 in Promax and −0.34 in direct Oblimin). Thus, we performed the Wherry hierarchical rotation, which yielded a single second-order factor (in this rotation, the interfactor correlation was −0.53). This dimension could be interpreted in terms of general inhibition (note that it was dominated by freezing) versus activity or boldness.

Separate factor analyses showed that the factor structures in spawning and nonspawning groups as well as in males and females were identical: values of several measures of factor matching (Ahmavaara factor invariance coefficient, Tucker congruence coefficient, Pearson correlation as well as the Kaiser–Hunka–Bianchini factor-matching coefficient and mean solution cosine, see Wherry 1984; Barrett 1986 for details) exceeded 0.89 (mean solution cosines between the two spawning groups and between the two sexes were 0.91 and 0.99, respectively). Thus, a single factor analysis, incorporating males and females as well as spawning and nonspawning individuals, was appropriate. Factor scores (regression estimates of both for the two Varimax factors and the second-order factor) were calculated for use in subsequent data analysis.

The latency to enter the inspection compartment correlated with primary and general factors (Krauth test: Freezing versus Activity: $W=18\,556$, $P<0.001$; Activity-Inspection versus Freezing: $W=-8632$, $P=0.068$; general factor: $W=-20\,554$, $P<0.001$), as did the latency to approach the novel fish (Krauth test: Freezing versus Activity: $W=10\,238$, $P=0.034$; Activity-Inspection versus Freezing: $W=-18\,046$, $P<0.001$; general factor: $W=-18\,310$, $P<0.001$). That is, active and uninhibited subjects were quicker to enter the unknown area and to approach the novel fish.

A factor analysis of the six mirror test variables (latency to the first interaction with the mirror, freezing, moving, escape, displaying and biting), using the above methodology, revealed two factors. However, the correlation matrix had low adequacy (Kaiser–Meyer–Olkin measure=0.58; even though $\chi^2_{15}=66.55$, $P<0.001$; spawning group: Kaiser–Meyer–Olkin measure=0.28, the matrix was close to singular and its inverse could not be computed in the nonspawning group) and no meaningful factor analysis of mirror test measures could be computed.

The latency to approach the mirror correlated moderately but significantly with the general factor: inhibited subjects had longer latencies ($r_S=-0.32$, $N=46$, $P=0.033$; but the lower-order factors showed only borderline significance levels: $P<0.11$). In addition, individuals hesitating to approach the mirror also hesitated to enter the novel compartment (Krauth test: $W=10\,505$, $P=0.026$), but not to approach the novel fish (Krauth test: $W=6356$, $P=0.187$). Finally, biting the mirror image conspecific and

displaying showed no correlations with the behavioural dimensions and latency to approach the mirror (all $Ps>0.1$). This was the case when the correlation analysis was performed separately for males and females.

Sex Differences in Behavioural Profiles

Two-way repeated measures ANOVA (sex as the repeated measures factor to control for within-pair relationships) showed a significant effect of sex (females were more active and less inhibited than males) but not of spawning group on the general factor (sex: $F_{1,21}=6.72$, $P=0.017$; spawning group: $F_{1,21}=0.06$, $P=0.81$; interaction: $F_{1,21}=0.08$, $P=0.79$). The same patterns were observed in the two primary factors, albeit the sex differences were not quite significant (Freezing versus Activity: $F_{1,21}=3.60$, $P=0.071$; Activity-Inspection versus Freezing: $F_{1,21}=3.26$, $P=0.085$). In the mirror test, females bit significantly more than males (two-way repeated measures ANOVA: sex: $F_{1,21}=4.50$, $P=0.046$, spawning group: $F_{1,21}=0.44$, $P=0.51$; interaction: $F_{1,21}=0.84$, $P=0.37$). There were, however, no differences between the sexes and spawning groups in displaying (all $Ps>0.5$). These results are consistent with previous data (e.g. Cole et al. 1980) indicating that female convict cichlids are bolder and more aggressive than males.

Behavioural Dimensions and Body Size

The spawning fish were significantly larger than nonspawning ones (Mann–Whitney U test: males: $U=18$, $N_1=13$, $N_2=10$, $P=0.005$; females: $U=3$, $N_1=13$, $N_2=10$, $P=0.0001$). Their standard length was correlated with behavioural factors, but only in males (all $Ps>0.25$ in females). In the spawning group, larger males had lower scores on the Activity-Inspection versus Freezing factor ($r_S=-0.82$, 95% confidence region $-1.00--0.59$, $N=13$, $P=0.001$). However, in the nonspawning group, larger males tended to be lower on the Freezing versus Activity factor ($r_S=-0.77$, 95% confidence region $-1.00--0.50$, $N=10$, $P=0.009$) and higher on the general factor ($r_S=0.63$, 95% confidence region $0.15-1.00$, $N=10$, $P=0.049$). It is difficult to interpret this conflicting result. Other variables were not significantly correlated with the standard length of the fish (all $Ps>0.25$).

Parental Behaviour and Behavioural Profiles

There were few significant correlations between behavioural profiles and patterns of parental behaviour, and they were sex specific. The aggregated parental food-provisioning (fin-digging) score did not correlate significantly with the behavioural factors ($Ps>0.1$), but showed a significant relationship with inspection of the novel fish ($r_S=0.63$, 95% confidence region $0.34-0.92$, $N=13$, $P=0.025$) and mirror test biting ($r_S=-0.62$, 95% confidence region $-0.95--0.30$, $N=13$, $P=0.027$) in males ($Ps>0.1$ in females).

The aggregated parental locomotion score correlated significantly with the Activity-Inspection versus Freezing factor in males ($r_S=-0.63$, 95% confidence region $-1.00--0.15$, $N=13$, $P=0.026$) but with Freezing versus Activity in females ($r_S=-0.61$, 95% confidence region $-1.00--0.22$, $N=13$, $P=0.029$). However, in both sexes, parental locomotion tended to be associated with open field freezing (males: $r_S=-0.57$, 95% confidence region $-0.96--0.18$, $N=13$, $P=0.048$; females: $r_S=-0.54$, 95% confidence region $-1.00-0.00$, $N=13$, $P=0.057$; both sexes combined: $r_S=-0.57$, $N=26$, $P=0.003$). There was also a significant negative correlation between parental locomotion and aggressive displaying to the mirror image in males ($r_S=-0.57$, 95% confidence region $-1.00--0.03$, $N=13$, $P=0.047$) but not in females ($P>0.5$).

The relationship between behavioural profile and time spent near the offspring depended on brood stage (note that this measure was not consistent over the breeding cycle). In females, the time spent near the brood at the first fry stage (3 days as fry) was negatively associated with the Freezing versus Activity factor ($r_S=-0.61$, 95% confidence region $-0.77--0.45$, $N=13$, $P=0.031$; $P>0.3$ in males) and no correlation was observed at other stages ($P>0.3$). The Activity-Inspection versus Freezing factor tended to correlate with the time spent near the brood at 17 days as fry in females ($r_S=0.56$, 95% confidence region $0.28-0.85$, $N=13$, $P=0.052$). Males showed the same trend ($r_S=0.47$, 95% confidence region $-0.03-0.97$, $N=13$, $P=0.10$), so that the relationship was significant when both sexes were combined ($r_S=0.57$, $N=26$, $P=0.002$). Additionally, more aggressive (biting in the mirror test) parents tended to spend more time away from their brood, but only when the fry were 17 days old (males: $r_S=-0.59$, 95% confidence region $-1.00--0.15$, $N=13$, $P=0.039$; females: $r_S=-0.67$, 95% confidence region $-1.00--0.29$, $N=13$, $P=0.013$).

Assortative Mating by Size and Behavioural Factors

There was an indication of extreme assortment of fish according to their body size in the spawning group (Table 2): larger males tended to form pairs and spawn with larger females. Furthermore, moderate albeit significant positive correlations were found between males and females in the behavioural factors (see Table 2). The latencies to enter the novel compartment (Krauth test: $W=456$, $P=0.004$, one tailed) and to approach the mirror ($r_S=0.52$, 95% confidence region $0.08-0.96$, $N=13$, $P=0.044$, one tailed) also correlated between the sexes. Thus, uninhibited males tended to mate with uninhibited females. However, there was no assortment in the latency to approach the novel fish and aggression measures ($Ps>0.44$). A completely different pattern was observed in the nonspawning fish. Here, no assortment was observed in the standard length, behavioural factors (Table 2) and behavioural latencies.

The observed assortment of breeding fish according to their behavioural profiles cannot be considered a simple by-product of the strong size assortment because the Freezing versus Activity factor, on which such assortment was obvious, did not correlate with the standard length of

Table 2. Spearman correlation coefficients between the standard lengths and between various behavioural factors of males and females within spawning and nonspawning pairs

	r_S	95% confidence interval of r_S	P*
Spawning pairs (N=13)			
Standard length	0.91	0.83–0.99	<0.001
Freezing versus Activity	0.57	0.22–0.91	0.029
Activity-Inspection versus Freezing	0.06	−0.59–0.71	0.436
General factor	0.49	−0.07–1.00	0.047
Nonspawning pairs (N=10)			
Standard length	0.03	−0.78–0.84	0.470
Freezing versus Activity	0.03	−0.54–0.60	0.473
Activity-Inspection versus Freezing	−0.02	−0.77–0.73	0.486
General factor	−0.31	−0.90–0.28	0.193

*One-tailed.

the fish. The general factor was also unrelated to fish size; yet it showed moderate assortment. Furthermore, partial Spearman correlations, adjusted for relationships with the standard length, were 0.48 for Freezing versus Activity, 0.51 for the general factor and 0.55 for the latency to approach the mirror. In addition, the pattern of assortative mating with respect to the latency measures (which were also unrelated to fish size) was consistent with their correlations with the behavioural factors: significant assortment was observed for the latencies that correlated more with the Freezing versus Activity factor or the general factor than with the Activity-Inspection versus Freezing factor.

DISCUSSION

Behavioural Dimensions

These results add to the growing literature documenting individual differences in various species (Slater 1981; Stevenson-Hinde 1983; Clark & Ehlinger 1987; Francis 1990; Benus et al. 1991; Magurran 1993; Wilson et al. 1994; Budaev 1997; Gosling 1998). Some behavioural dimensions are even similar across species (Mather & Anderson 1993; Wilson et al. 1994; Budaev 1997), for example, the shyness–boldness continuum (Wilson et al. 1994).

Recently, however, several authors (Wilson et al. 1994; Reed & Pizzimenti 1995; Coleman & Wilson 1998) have questioned whether individual differences really translate to various situations. Our results suggest that individual differences in the novelty and risk situations can be considered at several levels and may be general or specific depending on the level of analysis. Even though two different and situation-specific factors were extracted, a single higher-order dimension, presumably reflecting general behavioural inhibition, was also evident. Indeed, behaviour patterns associated with various motivations can be interfered with and suppressed by fear (Russell 1979; Boissy 1995). However, the behaviour of fish in novelty and risk situations showed relatively weak relationships with their behaviour in other contexts, such as aggression and parental care.

Behavioural inhibition and shyness often correlate negatively with aggressiveness (e.g. Carlstead 1981; Tulley & Huntingford 1988; Budaev 1997; see also Archer 1988 for a review), but our results indicate that they may be unrelated in the convict cichlid. This is probably associated with our use of the mirror test: unlike many studies we began recording only after the fish approached the mirror and started interacting with it. Therefore, aggression scores were not confounded with initial defensive responses in shyer individuals. In fact, the fish hesitating to approach the mirror also hesitated to enter the novel area and were generally more inhibited (had lower scores on the general factor).

Parental Style and Behavioural Profiles

The correlation between parental food provisioning and exploration found in males, and the negative correlation between provisioning and open field freezing, observed in both sexes, are consistent with the patterns documented in some other species. For example, the SAL strain of rats, *Rattus norvegicus*, which has high levels of exploration and active coping with stress and challenge (Benus et al. 1991), groom and nurse their pups more and stay alone less than the passive and shyer LAL rats (Benus & Röndigs 1996). Thus, behavioural inhibition is associated with lower levels of parental behaviour in other species, not only in the convict cichlid. This suggests that inhibition could translate to various situations and may affect parental behaviour. However, the relationships are not simple, since parental locomotion did not correlate with freezing in the novel fish test. Furthermore, males more active with the brood were less active in the presence of strange fish.

The correlation between the time spent away from the brood at the last brood stages and behavioural inhibition in the presence of the novel fish is difficult to understand. A possible hypothesis involves parental desertion by shyer parents. Provided competitive ability and dominance are associated with uninhibited and bold behavioural style (see Fox 1972; Francis 1984; Archer 1988; Verbeek et al. 1996), it may be adaptive for bold parents to defend territories and invest in active offspring care.

Inhibited individuals, presumably less able to defend good territories, could switch to a straying tactic and be more likely to engage in brood parasitism or 'farming out' (convict cichlids adopt broods which is adaptive for the adopters, see Wisenden & Keenleyside 1992). These behaviours would be facilitated by parental displacement.

Perhaps the most consistent result we obtained concerns the relationships between aggressiveness and parental care. Males showing more brood provisioning and parental activity were less aggressive (biting and displaying). In addition, parents (both males and females) who tended to stay away from their brood at the last fry stage for longer were also more aggressive in the mirror test. We suggest that aggressive parents could trade off brood defence against parental provisioning. A study in more naturalistic conditions should reveal whether aggressive parents concentrate on guarding the nest territory at a distance instead of more direct parental care.

Assortative Mating

Body size is considered an extremely important factor affecting reproductive success in various fish (see Turner 1993). Female convict cichlids prefer large males (Keenleyside et al. 1985) and males prefer large females (Nuttall & Keenleyside 1993) because large body size enhances competitive and nest defence abilities in males and increases fecundity in females. Indeed, size-assortative mating has already been documented in this species (Wisenden 1995). Our present results, revealing strong intrapair correlations in the spawning group are in agreement with this. The significant male–female correlations in behavioural inhibition versus general activity probably also reflect assortative mating. Because the non-spawning group (which paired but did not spawn) did not show such correlations, we may exclude the possibility that the correlations were a consequence of pairing and common maintenance of individuals for a prolonged time.

Further studies are needed to investigate the causes and consequences of assortative mating by behavioural profiles in fish. However, if behavioural inhibition versus activity, as measured in this study, is related to boldness, bold males should be more attractive to females (see Godin & Dugatkin 1996). Assortative mating may then be a consequence of sexual selection and competition for superior mates (Burley 1983). There may be other, but not necessarily exclusive, causes of assortment, such as behavioural compatibility, optimization of outbreeding (see Thiessen & Gregg 1980; Burley 1983; Crespi 1989 for reviews) or social learning (Freeberg 1996). The potential importance of assortative mating by behavioural profiles is emphasized by the observation that brood provisioning and parental locomotion were also closely correlated within pairs. Also, the time spent near the brood correlated within pairs at the beginning and end of the fry stage.

Conclusions

Our study revealed a complex pattern of relationships between parental behaviour and behavioural profiles in the convict cichlid. Individual differences in behavioural inhibition were relatively consistent across behavioural contexts but this was not the case for other behaviours. Moreover, the patterns of individual differences were complicated within the parental care and aggression situations. Further studies under more naturalistic conditions, including predators and conspecific competitors, are necessary to understand individual differences in these contexts more fully.

An important potential limitation of this study was that behavioural tests were conducted after the breeding period. Therefore, the behavioural profiles of the fish might have been affected by their mates, and their motivational states could have changed as a result of the parental care period 1 month before. A study reversing the testing order would be desirable to confirm the observed patterns, even though it would have its own limitations (e.g. behavioural testing involving stress could interfere with pair formation and subsequent reproductive behaviour). In addition, only one brood cycle was observed and the behavioural tests were also done only once. None the less, behavioural profiles correlated between parental and novelty situations separated by at least 1 month, indicating that some behavioural traits were consistent over that time. In fact, many behavioural traits in fish may show such continuity (e.g. Francis 1990; Budaev 1997).

References

Archer, J. 1988. *The Behavioural Biology of Aggression.* Cambridge: Cambridge University Press.

Atkinson, L. 1988. The measurement-statistics controversy: factor analysis and subinterval data. *Bulletin of the Psychonomic Society*, **26**, 361–364.

Barrett, P. 1986. Factor comparison: an examination of three methods. *Personality and Individual Differences*, **7**, 327–340.

Benus, R. F. & Röndigs, M. 1996. Patterns of maternal effort in mouse bidirectionally selected for aggression. *Animal Behaviour*, **51**, 67–75.

Benus, R. F., Bohus, B., Koolhaas, J. M. & van Oortmerssen, G. A. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, **47**, 1008–1019.

Boissy, A. 1995. Fear and fearfulness in animals. *Quarterly Review of Biology*, **70**, 165–191.

Brown, M. B. & Benedetti, J. K. 1977. Sampling behavior of tests for correlation in two-way contingency tables. *Journal of the American Statistical Association*, **72**, 309–315.

Budaev, S. V. 1995. EXPR: a computer system for the recording and analysis of animal behaviour. *Journal of Higher Nervous Activity*, **45**, 423–429 (in Russian).

Budaev, S. V. 1997. 'Personality' in the guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology*, **111**, 399–411.

Budaev, S. V. & Zhuikov, A. Y. 1998. Avoidance learning and 'personality' in the guppy (*Poecilia reticulata*). *Journal of Comparative Psychology*, **112,** 92–94.

Burley, N. 1983. The meaning of assortative mating. *Ethology and Sociobiology*, **4,** 191–203.

Carlstead, K. 1981. Motivational influences on individual and species differences in response to conspecifics in three *Haplochromis* species (Pisces: Cichlidae). Ph.D. thesis, University of Groningen.

Chandler, C. R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. *Animal Behaviour*, **49,** 524–527.

Clark, A. B. & Ehlinger, T. J. 1987. Pattern and adaptation in individual behavioral differences. In: *Perspectives in Ethology. Vol. 7. Alternatives* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 1–47. New York: Plenum.

Clutton-Brock, T. H. 1991. *The Evolution of Parental Care.* Princeton, New Jersey: Princeton University Press.

Cole, H. W., Figler, M. H., Parente, F. J. & Peeke, H. V. S. 1980. The relationship between sex and aggression in convict cichlids (*Cichlasoma nigrofasciatum* Günther). *Behaviour*, **75,** 1–21.

Coleman, K. & Wilson, D. S. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, **56,** 927–936.

Crespi, B. J. 1989. Causes of assortative mating in arthropods. *Animal Behaviour*, **38,** 980–1000.

Dziuban, C. D. & Shirkey, E. S. 1974. When is a correlation matrix appropriate for factor analysis? Some decision rules. *Psychological Bulletin*, **81,** 358–361.

Fox, M. W. 1972. Socio-ecological implications of individual differences in wolf litters: a developmental and evolutionary perspective. *Behaviour*, **41,** 298–313.

Francis, R. C. 1984. The effects of bidirectional selection for social dominance on agonistic behavior and sex ratios in the paradise fish (*Macropodus opercularis*). *Behaviour*, **90,** 25–45.

Francis, R. C. 1990. Temperament in a fish: a longitudinal study of the development of individual differences in aggression and social rank in the Midas cichlid. *Ethology*, **86,** 311–325.

Freeberg, T. M. 1996. Assortative mating in captive cowbirds is predicted by social experience. *Animal Behaviour*, **52,** 1129–1142.

Godin, J.-G. J. & Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences U.S.A.*, **93,** 10 262–10 267.

Gosling, S. D. 1998. Personality dimensions in spotted hyenas (*Crocuta crocuta*). *Journal of Comparative Psychology*, **112,** 107–118.

Keenleyside, M. H. A., Rangeley, R. W. & Kuppers, B. U. 1985. Female mate choice and male parental defense behaviour in the cichlid fish *Cichlasoma nigrofasciatum*. *Canadian Journal of Zoology*, **63,** 2489–2493.

Kimmel, H. D. 1957. Three criteria for the use of one-tailed tests. *Psychological Bulletin*, **54,** 351–353.

Krauth, J. 1988. *Distribution-free Statistics: An Application Based Approach.* Amsterdam: Elsevier.

Maestripieri, D. 1993. Maternal anxiety in rhesus macaques (*Macaca mulatta*) II. Emotional bases of individual differences in mothering style. *Ethology*, **95,** 32–42.

Magurran, A. E. 1993. Individual differences and alternative behaviours. In: *The Behaviour of Teleost Fishes* (Ed. by T. J. Pitcher), pp. 441–477. London: Chapman & Hall.

Mather, J. & Anderson, R. C. 1993. Personalities of octopuses (*Octopus rubescens*). *Journal of Comparative Psychology*, **107,** 336–340.

Nuttall, D. B. & Keenleyside, M. H. A. 1993. Mate choice by the male convict cichlid (*Cichlasoma nigrofasciatum*, Pisces, Cichlidae). *Ethology*, **95,** 247–256.

Reed, P. & Pizzimenti, L. 1995. Lack of consistent individual differences in rats on tasks that require response inhibition. *Animal Learning and Behavior*, **23,** 454–460.

Russell, P. A. 1979. Fear-evoking stimuli. In: *Fear in Animals and Man* (Ed. by W. Sluckin), pp. 86–124. New York: Van Nostrand Reinhold.

Slater, P. J. B. 1981. Individual differences in animal behavior. In: *Perspectives in Ethology. Vol. 4. Advantages of Diversity* (Ed. by P. P. G. Bateson & P. H. Klopfer), pp. 35–49. New York: Plenum.

Stevenson-Hinde, J. 1983. Individual characteristics. A statement of the problem. Consistency over time. Predictability across situations. In: *Primate Social Relationships: An Integrated Approach* (Ed. by R. A. Hinde), pp. 28–34. Oxford: Blackwell.

Thiessen, D. & Gregg, B. 1980. Human assortative mating and genetic equilibrium: an evolutionary perspective. *Ethology and Sociobiology*, **1,** 111–140.

Tulley, J. J. & Huntingford, F. A. 1988. Additional information on the relationship between intra-specific aggression and anti-predator behaviour in the three-spined stickleback, *Gasterosteus aculeatus*. *Ethology*, **78,** 219–222.

Turner, G. F. 1993. Teleost mating behaviour. In: *The Behaviour of Teleost Fishes* (Ed. by T. J. Pitcher), pp. 307–331. London: Chapman & Hall.

Verbeek, M. E. M., Boon, A. & Drent, P. J. 1996. Exploration, aggressive behavior and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour*, **133,** 945–963.

Wherry, R. J. 1984. *Contributions to Correlational Analysis.* New York: Academic Press.

Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107,** 250–260.

Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, **9,** 442–446.

Wisenden, B. D. 1995. Reproductive behaviour of free-ranging convict cichlids, *Cichlasoma nigrofasciatum*. *Environmental Biology of Fishes*, **43,** 121–134.

Wisenden, B. D. & Keenleyside, M. H. A. 1992. Intraspecific brood adoption in convict cichlids: a mutual benefit. *Behavioral Ecology and Sociobiology*, **31,** 263–269.

Wisenden, B. D., Lanfranconi-Izawa, T. L. & Keenleyside, M. H. A. 1995. Fin digging and leaf lifting by the convict cichlid, *Cichlasoma nigrofasciatum*: examples of parental food provisioning. *Animal Behaviour*, **49,** 623–631.

Wright, S. P. 1992. Adjusted P-values and simultaneous inference. *Biometrics*, **48,** 1005–1013.

Zwick, W. R. & Velicer, W. F. 1986. Comparison of five rules for determining the number of components to retain. *Psychological Bulletin*, **99,** 432–442.

Zworykin, D. D. 1998. Parental fin digging by *Cichlasoma octofasciatum* (Teleostei: Cichlidae) and the effect of parents' satiation state on brood provisioning. *Ethology*, **104,** 771–779.

Zworykin, D. D., Budaev, S. V. & Mochek, A. D. 1998. Alternative tactics of male compensatory behaviour during parental care in *Cichlasoma octofasciatum* (Teleostei: Cichlidae). *Marine and Freshwater Behaviour and Physiology*, **31,** 185–191.