Boldness, aggression and exploration: evidence for a behavioural syndrome in male pentamorphic livebearing fish, *Poecilia parae*

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Abstract. A body of evidence is being accumulated on consistent individual differences in behaviour for several animal taxa. Individuals of these species exhibit different levels of risk during competition over limited resources, and the resultant behavioural types perform better under different social and physical environmental conditions. We used approach distance to a model of a piscivore predator the pike cichlid (*Crenicichla saxatilis*) to categorize male pentamorphic livebearing fish or pentas (*Poecilia parae*) as bold, intermediate, and shy, and then tested the hypothesis that when behaviours are correlated, individuals express different behaviour types under different contexts. Our results for the most part corroborated the six predictions generated by the aforementioned hypothesis: (1) bold pentas explored a T-maze in the shortest time, and initially approached the chamber with a living pike cichlid instead of the one with the conspecific male; (2) intermediate pentas spent more time exploring the maze and exhibited no initial interest in the predator chamber nor the conspecific one; (3) shy individuals spent the most time exploring the maze, and initially approached the predator chamber, providing only partial support for this prediction because shy males did not initially approach the conspecific chamber; (4) approach distance from the pike cichlid predator model and time to explore the maze was positively correlated; (5) bold pentas exhibit highest levels of aggression toward conspecifics; and (6) bold individuals ingested the most conspecific fry. Our results lead to the conclusion that pentas exhibited a behavioural syndrome with bold fish being more aggressive, faster explorers of novel situations, and more cannibalistic than intermediate and shy individuals of the same population. Thus, penta males fall into a behavioural syndrome formally known as the proactive-reactive axis.
Key Words: aggression, behavioural type, personality, Poeciliidae, proactive-reactive axis, shyness.

Tartalom. Az idök során, sok adat gyült az állati populaciok egyénei közötti viselkedesi jellemvonásokról. Egy faj egyénei, számos veszélynek vannak kitéve a gátlott élelemforrások megszerzésében, ezért a viselkedési salyátosságok hangsulyozottabbak a külömböző szociális, fizikai és környezeti feltételek közt. A fentieken alapozva kisérletünk során megpróbáltuk osztályozni a *Poecilia parae* halfajt a következő csoprtokba: bátrak, ovatosak és félenkek. Ezt a felosztást, egy ragadozó halfajhoz (*Crenicichla saxatilis*) való közeledési távolság megfigyelésén keresztül probáltuk elérni. Ugyanakkor ellenőriztük azt a feltételezést is, hogy akkor, amikor a viselkedési jellemvonások kapcsolatban vannak egymással, az egyének eltérő viselkedést nyilványitank külömböző helyzetekben. Kisérletünk eredményei nagyrész megfeleltek az elöbb emlitett feltételezes elméleti végkifutásaival: (1) a bátor egyének a T alaku labirintust a legrövidebb idő alatt haladták végig, illetve bátran közeledtek a ragadozó cellájához, elkerülve a fajukhoz tartozó him celláját, (2) az ovatos egyének hosszabb idöt töltöttek a labirintus áthaladásával és nem nyilványitottak kezdetben semmi érdeklödést, sem a ragadozó, sem a fajukhoz tartozó egyén cellája iránt, (3) a félénkek csoportjából a megfigyelt egyének a leghosszabb idő alatt haladták át a labirintust, azonban a ragadozó cellájához közeledtek elöbb, ez a tény csak részben támasztotta alá elvárásainkat hisz a him cellájához való kőzeledés volt elvárható és a legvalószinübb, (4) a ragadozóhoz való közeledési távolság, illetve a labirintus áthaladásának ideje pozitiv összefüggésben voltak egymással, (5) a bátor egyének agresszivitása jelentös volt a salyát falyukhoz tartozó egyénekkel szemben, (6) a bátrak csoportjához tartozó egyének kanibalizmusszintje volt a legnagyobb. Kisérleteink azt a következtetest körvonalazzák, hogy a *Poecilia parae* halfaj azt a viselkedesi szindrómát nyilványitja, hogy a bátrak csoportjához tartozó egyének agresszivebbek, hamarabb fölkutatják az ujonnan adodó helyzeteket, illetve kanibalizmusszintjük sokkal nagyobb mint az ovatosak vagy félenkek csoportjához tartozó egyénéké.
Kulcsszavak: agresszivitás, viselkedési tipusok, egyéniség, Poeciliidae, ovatoság.

Rezumat. O seamă de date s-au acumulat cu privire la diferenţele comportamentale semnificative observate între indivizii aceleiaşi populaţii la câţiva taxoni animali. Indivizii acestor specii manifestă diferite grade de risc în timpul competiţiei pentru limitatele resurse de hrană, iar tipurile comportamentale rezultante operează mai bine în diferitele condiţii sociale, fizice şi ambientale. Noi am luat în calcul distanţa la care s-au apropiat indivizii de un model de prădător piscivor (*Crenicichla saxatilis*) pentru a împărţi indivizii speciei de peşti ovovivipari *Poecilia parae,* sau penta, în următoarele categorii de indivizi: îndrăzneţi, intermediari şi precauţi, iar apoi am testat ipoteza conform căreia atunci când comportamentele sunt corelate, indivizii manifestă diferite tipuri comportamentale în contexte diferite. Rezultatele noastre, în cea mai mare parte, au concordat cu cele şase predicţii generate de ipoteza anterior menţionată: (1) indivizii îndrăzneţi au explorat un labirint T în cel mai scurt timp şi s-au apropiat mai întâi de camera prădătorului cichlid şi nu în cea cu un conspecific mascul; (2) indivizii intermediari au petrecut mai mult timp explorând labirintul şi nu au manifestat, iniţial, interes nici pentru camera cu prădător nici pentru cea cu conspecificul lor; (3) cei precauţi au petrecut cel mai mult timp explorând labirintul, dar iniţial s-au apropiat de camera cu prădător, susţinând doar parţial predicţia noastră, deoarece, conform aşteptărilor, aceştia ar fi trebuit să se apropie mai mult de camera cu individul conspecific; (4) distanţa de apropiere de prădătorul cichlid model şi timpul de explorare a labirintului au fost corelate pozitiv; (5) indivizii îndrăzneţi au manifestat cel mai ridicat grad de agresivitate faţă de conspecifici; (6) tot cei îndrăzneţi au fost cei care au consumat numărul cel mai mare de pui conspecifici. Rezultatele noastre conduc la trasarea concluziei că peştele penta manifestă un „sindrom comportamental" în care indivizii îndrăzneţi sunt mai agresivi, mai rapizi exploratori ai situaţiilor noi şi mai canibali decât indivizii intermediari şi precauţi ai aceleiaşi populaţii. Astfel, masculii de peşti penta se încadrează în rândul celor cu „sindrom comportamental", model cunoscut şi sub numele de „axa proactivă-reactivă".

Cuvinte cheie: agresivitate, tipuri comportamentale, personalitate, Poeciliidae, axa proactivă-reactivă, precauţie.

Introduction. Several recent papers are providing evidence that individuals differ in suites of correlated behavioural traits (Wilson 1998; Fraser et al 2001; Gosling 2001; Dingemanse et al 2003; Sih et al 2003; Bell & Stamps 2004; Bell 2007; Stamps 2007; Wolf et al 2007). Individual differences in boldness, aggression, exploration, risk aversion and other personality traits in animals are consistent and stable for reasons that until recently defied theoretical explanation (see Stamps 2007; Wolf et al 2007). Combinations of these personality traits formally known as behavioural sindromes when expressed by populations, are correlations between behaviours in different functional contexts (Sih et al 2004a,b; Bell 2007). Thus, individuals who are more aggressive toward conspecifics, might also be too aggressive toward predators, prey, and their progeny (Sih et al 2004a,b; Bell 2007; Stamps 2007; Wolf et al 2007). When behaviours are correlated, individuals exhibit different behavioural types such that some are bold and aggressive, while others are shy and nonaggressive (Sih et al 2004a,b; Bell 2007). Behavioural syndromes are attracting attention because they have several important evolutionary and ecological implications (Bell et al 2006). Yet, the implication that has generated the most controversy is that behavioural syndromes might be responsible for apparently maladaptive behaviour, so that a tendency to be generally bold and aggressive might carryover to cause individuals to be inappropriately aggressive in some situations (Bell 2007).

Interest in behavioural syndromes is growing because correlations among behaviours could impose a limit on optimal behaviour through either developmental or evolutionary time (Sih et al 2004a,b; Bell & Stamps 2004; Bell 2007; Wolf et al 2007). Thus, if two behaviours are strongly linked because they are both influenced by common, underlying physiological processes, then these behaviours cannot change independently, and the correlation between them might be difficult to uncouple (Bell & Stamps 2004; Bell 2007; Stamps 2007; Wolf et al 2007). We should therefore expect to see the same association between behaviours in different contexts (Sih et al 2004a,b; Bell 2007; Stamps 2007; Wolf et al 2007).

Our aim was to use predator inspection behaviour (Pitcher et al 1986; Dugatkin & Godin 1992; Watson-Rodney 2005) to characterize the behavioural type of individual male pentamorphic livebearing fish or pentas (*Poecilia parae*, Eigenmann) as bold, intermediate, and shy. These phenotypes were then used to test the hypothesis that when behaviours are correlated, individuals express different behaviour types under different contexts (Sih et al 2004a,b; Bell 2007). This hypothesis generated six predictions that gain their validity from several empirical studies as follows: (1) bold

pentas should explore a T-maze in the shortest time, and initially approach the chamber with a live pike cichlid (*Crenicichla saxatilis* (Linnaeus)) instead of the conspecific male side; (2) intermediate pentas should take longer to explore the maze and show no initial interest in the predator chamber or the conspecific side; (3) shy individuals should take the most time to explore the maze, and initially approach the conspecific chamber; (4) approach distance from the pike cichlid predator model and time to explore the maze should be positively correlated, and bold fish should exhibit the highest correlation coefficient; (5) bold fish should exhibit higher levels of aggression toward conspecifics than either intermediates or shy individuals; and (6) bold individuals should ingest many more conspecific fry than either intermediate or shy males (Huntingford 1976; van Oortmerssen & Busser 1989; Benus et al 1991; Hessing et al 1993; Fraser et al 2001; Malmkvist & Hansen 2002; Dingemanse et al 2003, 2004).

Materials and Methods. Penta males occur in five distinct morphs (Figure 1), colorful *melanzona* (blue, red, yellow), and a less colorful *parae* with color in the caudal and dorsal fins, and a female-like *immaculata* (Liley 1966; Lindholm et al 2004). All five morphs used in experiments described below were wild caught from a high-predation ditch system in the village of West Patentia (6°41.633′ N, 58°11.963′ W), Guyana, South America. Fish were caught by dipnets (Bourne et al 2003) in three connected small ditches on 20 June 2004 and 28 May 2006, and were housed and maintained as described in Bourne et al (2003) at the laboratory at CEIBA Biological Center (06° 29.928′ N, 58° 13.111′ W).
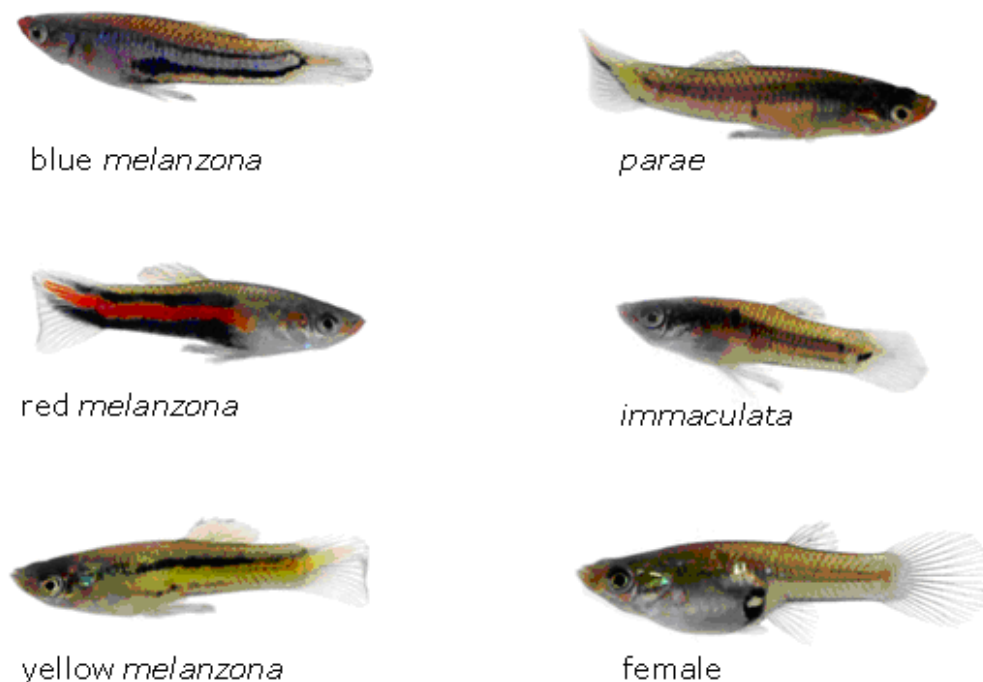

Figure 1. The five male morphs and female pentamorphic livebearer, *Poecilia parae*, exhibiting extreme discrete color pattern polymorphism and sexual dimorphism typical of this species and many livebearers or poeciliids which includes the popular aquarium fish, the guppy, *P. reticulata* Peters.

On 23-28 June 2004, during 0830-1200h we tested 120 well-fed male *P. parae* for their tendency to inspect a Storm WildEye Swim Bait Shad® (100 mm standard length, SL × 25 mm W), painted to resemble a pike cichlid a major predator of *P. parae*, and on 29-31 May 2006 an additional 60 males were similarly tested. A modification of the estimation of boldness method of Brick & Jakobsson (2002) was used. Observations were made in a tank (50.8 cm × 25.2 cm × 31 cm and filled to a depth of 11 cm) containing a 25 mm

layer of gravel (Figure 2). The predator faced the *P. parae* release chamber at one end of the tank. An area 50 mm all around the predator was delineated by differently sized gravel and a series of 2 mm diameter palm frond petioles set at specific distances from the predator (see definitions below), used to assess distances from the predator by focal *P. parae*. A school consisting of two females and two males was placed in the opposite end chamber to provide the social stimulus for focal males to perform anti-predator behaviors (Magurran et al 1992). A focal male was placed by dip net in the holding chamber of the test tank, and allowed 5 min to acclimate. After remote release, he had to swim about 45 cm to the other end of the aquarium to pass the predator, and interact with the school. We observed the behavior of each male for 15 min as in Brick & Jakobsson (2002). Boldness and shyness are extremes of the same trait - a propensity to take risks in novel or challenging situations (Wilson et al 1994). However, we operationally defined boldness by categorizing each male as: (1) "bold" if he approached the model predator for ≥121 s at a range of from ≤50-110 mm; (2) "shy" if individuals inspected for ≤ 30 s at 141-175 mm. Although shy, males that never swam to the school were not used in experiments; and (3) "intermediate" if inspection ranged from 31-120 s at 111-140 mm.
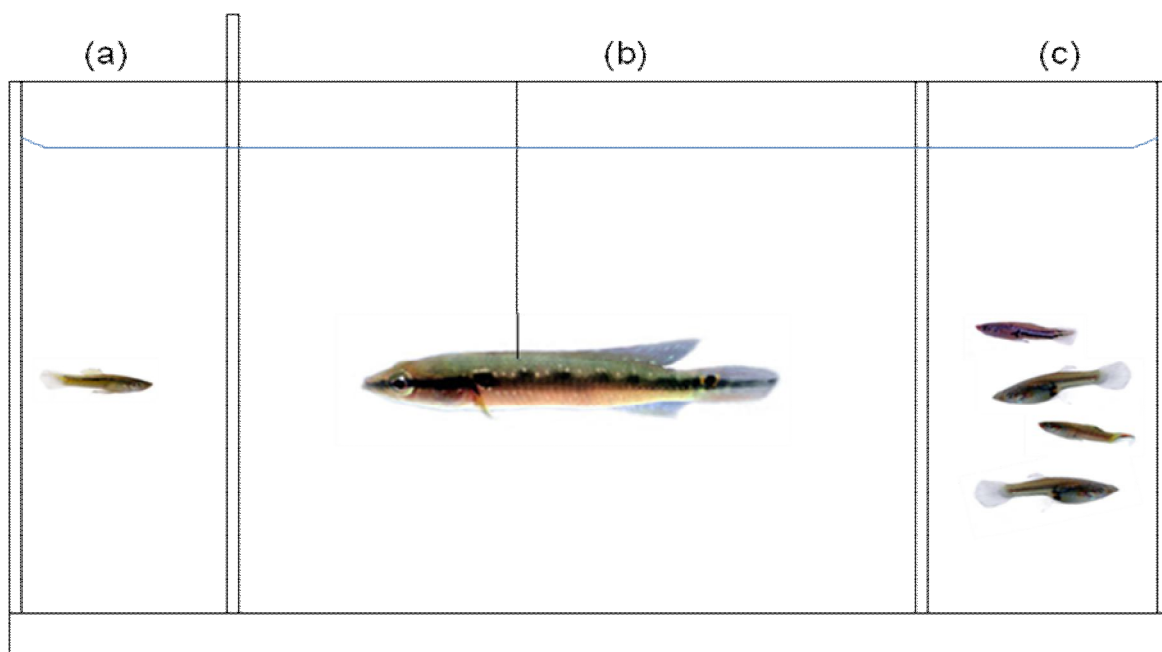

Figure 2. Schematic representation of a 38-l aquarium used to categorise pentas, *Poecilia parae* as bold, intermediate, or shy. (a) test subject release chamber with a yellow *melanzona* morph, (b) predator chamber with a model of a pike cichlid, *Crenicichla saxatilis*, and (c) companion chamber with blue *melanzona* and *parae* male morphs, and two females.

Another aquarium (50.8 cm × 25.2 cm × 31 cm and filled to a depth of 11 cm) was equipped with a sealed glass T-maze measuring 50 cm long × 9 cm wide. All sides of the outer aquarium were wrapped in wax paper to reduce distractions for all fish. The two sealed end chambers at the top of the T were 11 cm × 8 cm. We randomly assigned a satiated small pike cichlid (*Crenicichla saxatilis*), 58 mm standard length (SL) that was maintained on live male guppies, to one of these chambers, and a *parae* morph to the other for each test. The live pike cichlid represented the novel stimulus and the *parae* male was the social stimulus for the randomly presented bold, intermediate, and shy phenotypes undergoing individual testing in the maze. During 1-6 July 2004, we randomly presented one-at-a-time, 90 satiated *P. parae* 17.9 ± 1.4 mm SL, to determine whether 30 of each personality type made the predicted initial approaches to either the chamber containing the pike cichlid or the conspecific male. These individuals were run

through the T-maze beginning at the base of the T, and timed by stopwatch. We repeated this experiment during 1-3 June 2006 using 15 males of each boldness level.

To determine whether there were differences in time to explore the T-maze by personality type, median time (s) spent exploring the maze (dependent) was analyzed by a Kruskal-Wallis ANOVA with Dunn's multiple comparisons test, because these data were not normally distributed even after transformations. Spearman's correlation was used to determine whether the relationship between approach distance from the predator model and time to explore the maze was positively correlated. Finally, a 3×2 contingency table was used in a χ^2 goodness of fit analysis to test the observed proportions for initial approaches towards the predator or conspecific chambers. We predicted that initial approach should differ for each type in the bold syndrome, with null expectations of 51:49 for bold fish preferring the predator chamber, 50:50 for intermediate individuals, and 51:49 for the shy phenotype preferring the conspecific chamber.

During the July 2004 tests, shy fish did not behave as predicted in maze exploration. Thus, the 22 surviving shy *P. parae* were retested by GRB with the model predator and in T-maze during 10-12 November 2004. To determine whether the 22 surviving shy fish retested as shy, approach distance from the model data were used in an unpaired t-test model to examine means of 22 randomly selected original data points and recent approach distances. A Mann-Whitney U test was applied to the medians of time to explore the T-maze, and a 2×2 contingency table was examined by a Fisher's Exact test to determine whether row and column associations for original chamber and retested initial approaches were different.

During 4-7 June 2006, four of us each observed and recorded aggressive behaviour (numbers of nibbles and/or butts) delivered by the 15 bold, 15 intermediate, and 15 shy focal individuals used in the T-maze tests earlier. The test arena consisted of four 7.6-l aquaria in which were housed a randomly selected group of three males not of the same color morph as the focal male (*sensu* Altmann 1974) and three females to determine levels of conspecific aggression by the focal male during a 10 min period. All individuals were changed after each test. In addition, 40 pregnant females were individually housed in small deli-cups to provide fry for the experiment to determine whether bold males ingested more conspecific fry than either intermediate or shy males. Females were removed from deli-cups when fry appeared in the cups. Ten fry about 48 h old were placed in each of the deli-cups holding a male fasted for 48 h and of known boldness level and the number remaining after 10 min was subtracted from 10 to determine the number ingested by each focal male.

Results and Discussion. Bold *P. parae* explored the T-maze in the shortest time (KW = 26.393, P > 0.0001, with Dunn's multiple comparisons test indicating that significant differences were partitioned for bold time vs. intermediate time, P < 0.05, bold time vs. shy time, P < 0.001, and intermediate time vs. shy time, P < 0.05; Figure 3a). Moreover, bold fish exhibited the predicted initial approach to the chamber with the live pike cichlid instead of the chamber with the conspecific male (χ^2 = 15.45, df = 2, P = 0.0004; first pair of bars Figure 3b). Intermediate *P. parae* took significantly longer to explore the maze than bold individuals (Figure 3a), and made no initial approach to either chamber (second pair of bars Figure 3b). Shy individuals took significantly more time to explore the maze than bold or intermediate individuals (Figure 3a), and did not approach the conspecific chamber (last pair of bars Figure 3b).
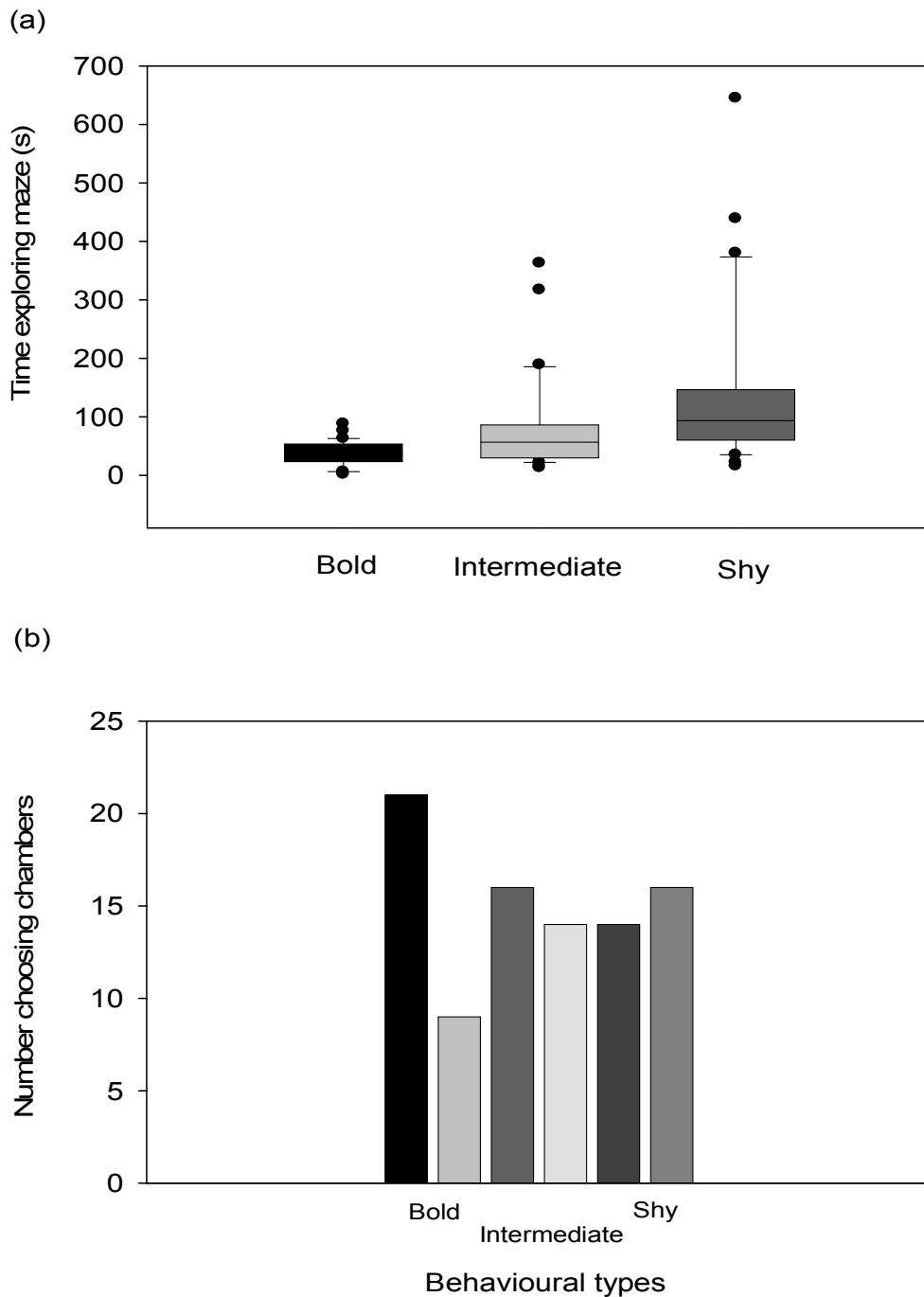
Figure 3a. Box plots in which the boxes depict the 10th, 25th, 75th, and 90th percentiles, horizontal lines within the boxes are medians, and whiskers are error bars estimated from column means of travel times for bold, intermediate and shy pentas (*Poecilia parae*) exploring a T-maze. Closed circles display extreme values. Figure 3b. Frequency distributions of the number of individuals of each behavioural type that initially visited the pike cichlid (*Crenicichla saxatilis*) predator chamber (darker bars in all pairs) and conspecific chamber (lighter bars) of the T-maze, respectively. The first pair of bars is for bold pentas, second pair for intermediate fish, and the third pair is for shy individuals.

Approach distance from the pike cichlid predator model and time to explore the T-maze were positively correlated, and bold *P. parae* had the highest correlation coefficient compared to intermediate and shy phenotypes (Figure 4).
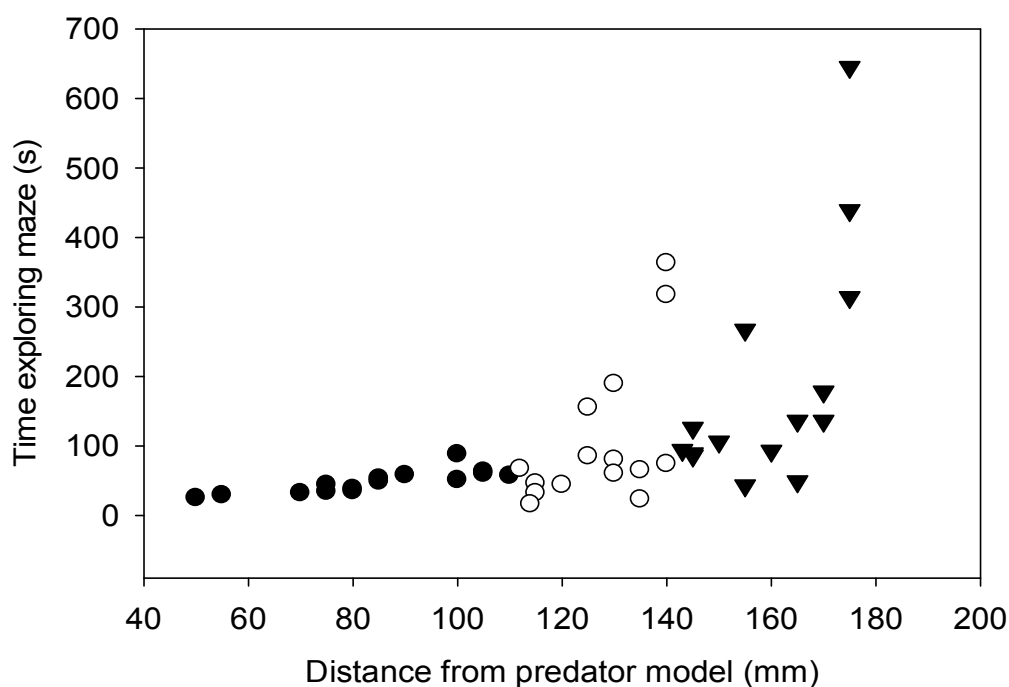
Figure 4. The correlation between time it took male pentas (*Poecilia parae*) to explore = swim a T-maze and initially choose a predicted chamber on approach distances from predator model; ● bold fish ($r_s = 0.82$, P = 0.006), ○ intermediate fish ($r_s = 0.52$, P = 0.05), and ▼ shy fish ($r_s = 0.66$, P = 0.01).

On retesting, the 22 surviving shy fish did not approach the model predator closely (July, 162 ± 11 mm and November, 161 ± 11 mm, $t_{42} = 0.574$, P = 0.57), did not differ in maze exploration time (medians 95 s for July and 101 s for November, MWU = 228.50, P = 0.76, n = 22), and did not initially approach the conspecific chamber (July, 14:16, November, 11:11, Fisher's Exact test, P = 1.00).

Our results indicated the existence of variable animal personality because on one hand, bold males as predicted explored the maze in the shortest time, and initially approached the chamber with the live pike cichlid instead of the side with a live conspecific male. And lends support for validation of the boldness classification method. On the other hand, intermediate pentas took significantly more time to explore the maze and did not initially approach the predator chamber or the conspecific side of the maze, while shy males took the most time to explore the maze, but did not initially approach the conspecific chamber as predicted. Our data also indicated behaviour repeatability in both the predator inspection categorization and in the maze exploration tests by the 22 surviving shy pentas 5 months later. Furthermore, Dugatkin & Godin (1992) indicated that some guppies consistently tested as bold while others tested as shy. More recently in 2007 and 2008, pentas and South American mollies (*P. vivipara* Bloch & Schneider) retested as bold, intermediate, and shy 5 mo and 2 mo respectively (G. R. Bourne unpubl. data). Thus, the personality traits of some poeciliids seem to be stable over at least short time spans.

But why should shy pentas that maintained considerable distance from the stationary model predator (a novel situation) in the personality assessment test show such an interest in a live pike cichlid in the T-maze test? Since shyness and boldness are extremes of the same behavioural trait they are probably strongly linked because they may both be influenced by common, underlying physiological processes, so they cannot change independently, and the correlation between them might be difficult to uncouple (Bell & Stamps 2004; Bell 2007; Stamps 2007; Wolf et al 2007) under these circumstances, we should expect to see the same association between behaviours in different contexts (Sih et al 2003; Sih et al 2004a,b; Bell 2007; Stamps 2007; Wolf et al

2007). Thus, some shy individuals responded to the small live pike cichlid by approaching closely which was quite different to their behaviour of avoidance of the novel non-mobile model predator.

Our data also corroborated Prediction (4), that approach distance from the pike cichlid predator model and time to explore the T-maze was positively correlated. However, we also found that bold pentas had the highest correlation coefficient compared to intermediate, and shy morphs. Taken as a whole, our results indicated correlations between boldness towards a model and live predator and exploration of a T-maze by pentas. Male pentas which were bold in inspecting the model predator also had the shortest times exploring the T-maze, and initially approached the test chamber with the live predator instead of the conspecific.

Bold pentas were more aggressive towards unfamiliar male and female conspecifics than were either intermediate or shy behavioural types (Figure 5a; KW = 31.11, P < 0.0001, n = 15 males), and bold males also ingested more conspecific fry than did intermediate and shy males (Figure 5b; KW = 34.98, P < 0.0001, n = 15 males). In addition, Wilcoxon matched-pairs signed-ranks tests indicated that medians of the differences between the number of aggressive acts and the number of fry eaten by bold (P = 0.03; pairings were highly correlated, r_s = 0.89), intermediate (P = 0.0001, pairings were highly correlated, r_s = 0.82), and shy (P = 0.0078; pairings were correlated, r_s = 0.61) pentas differed significantly from zero.

Our results further indicated strong support for predictions of aggression toward adult and young conspecifics because bold fish exhibit higher levels of nibbling and/or butting of unfamiliar individuals than either intermediates or shy pentas, and bold individuals ingest many more fry than either intermediate or shy males. This seemingly maladaptive behaviour of cannibalizing fry many of which might be progeny, now makes sense in light of the very recent theoretical findings of life-history trade-offs (Roff 2001) between growth and mortality which can favour the evolution of personality (Stamps 2007). In this scenario, individuals can either grow fast but risk dying young, or play it safe and grow slowly but enjoy a longer life-span; this ensues because individuals that can benefit from growing at a consistent rate by ingesting conspecific young while reducing risks of mortality will be favoured (Stamps 2007; Smith & Blumstein 2008). Thus, all things being equal, bold and aggressive male pentas should enjoy a fitness advantage over intermediate and shy males that are less aggressive and less likely to ingest conspecific fry. However, since things are usually not equal as Stamps (2007) illustrated, both the fast- and slow-growing strategy can be maintained in a population when the two strategies have equal fitness owing to a trade-off with mortality. Thus, the type of behavioural variation seen in the penta system presented here can result (see Wilson 1998; Smith & Blumstein 2008).

Conclusions. In summary, we present strong evidence corroborating the hypothesis that when behaviors are correlated, individuals express different behavior types under different contexts; because bold pentas explored a T-maze in the shortest time, and initially approached the chamber with a living pike cichlid instead of the conspecific male displaying a willingness to expose themselves to risk of predation. Intermediate pentas spent more time exploring the maze and exhibited no initial interest in the predator chamber nor in the conspecific one. Shy individuals took the longest exploring the maze, and initially approached the predator chamber. However, there was only partial support for the prediction because shy males did not initially approach the conspecific chamber. Furthermore, approach distance from the pike cichlid predator model and time to explore the maze was positively correlated, with bold fish exhibiting the highest correlation coefficient providing validation of the boldness classification method. Bold pentas exhibited the highest levels of aggression toward conspecifics, and even ingested the most conspecific fry. Thus this population of pentas exhibited a behavioural syndrome because bold fish were more aggressive, faster explorers of novel situations, and more cannibalistic than intermediate and shy individuals. Penta males clearly fall into a behavioural syndrome formally known as the proactive-reactive axis (Koolhass et al 1999; Reale & Festa-Bianchet 2003), and is documented in several other species

(Huntingford 1976; van Oortmerssen & Busser 1989; Benus et al 1991; Hessing et al 1993; Fraser et al 2001; Malmkvist & Hansen 2002; Dingemanse et al 2003, 2004; Huntingford & Adams 2005). In any case, the proactive-reactive behavioural syndrome is evolutionarily significance because aggressive and bold, proactive individuals, readily explore their environment, manipulate social and physical environmental challenges, and easily adopt persistent routines (Wilson 1998; Sih et al 2004a). On the other hand, those of the reactive phenotype track external stimuli closely, adjusting warily to changes in the environment (Sih et al 2004a,b). These contrasting coping styles apparently represent alternative, coherent, adaptive strategies (Koolhass et al 1999; Sih et al 2004a,b; Smith & Blumstein 2008).

(a)

(b)
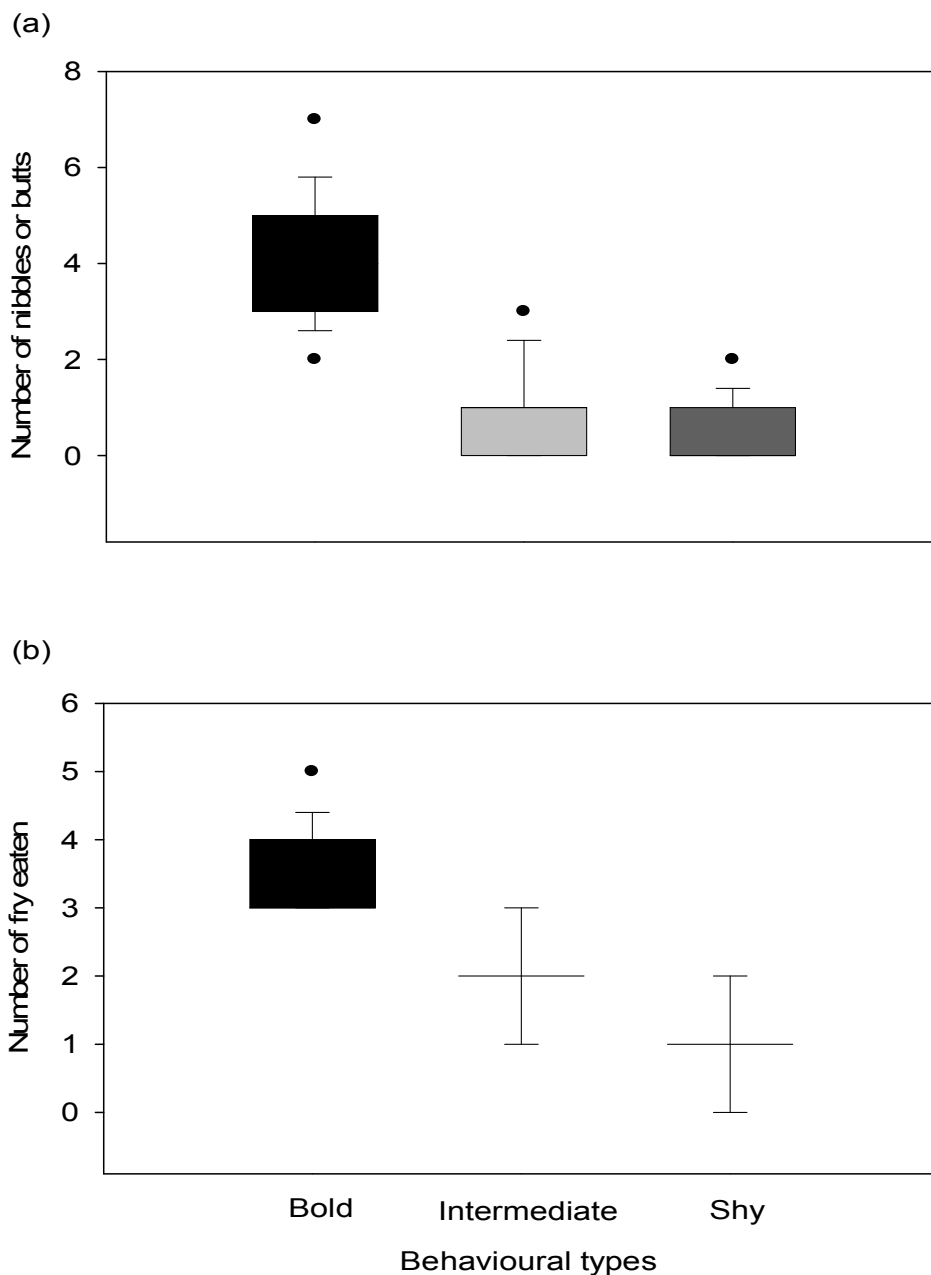
Figure 5a. Box plots of numbers of nibbles and/or butts delivered by males to unfamiliar adult pentas (*Poecilia parae*) in an assessment of aggression by bold, intermediate, and shy behavioural types. Figure 5b. Box plots showing the number of fry eaten to assess cannibalism by the bold, intermediate and shy individuals. In both figures, boxes depict the 10th, 25th, 75th, and 90th percentiles, horizontal lines are medians, whiskers are error bars estimated from column means, and solid circles are extreme values.

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