Individual Differences in Exploratory and Antipredator Behaviour in Juvenile Smallmouth Bass (Micropterus Dolomieu)

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Individual differences in exploratory and antipredator behaviour in juvenile smallmouth bass 
(*Micropterus dolomieu*)

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(Accepted: 3 August 2008)

Summary

The correlation of individual behaviour in different contexts, known as a behavioural syndrome, constrains the optimization of behaviour within each context. Recent studies reveal that the strength of syndromes differs amongst populations and over individual ontogeny. In this study, exploratory behaviour in an unfamiliar environment and behavioural responses to a simulated predator attack in the presence of food were measured in juvenile smallmouth bass (*Micropterus dolomieu*). The results revealed a syndrome: individuals who actively explored the unfamiliar environment also behaved more boldly in the presence of the model predator. The syndrome implies a tradeoff between collecting information about one’s environment and risk of a predator attack. Additionally, the results revealed different anti-predator strategies. The simulated predator attack induced a longer period of activity (presumably to disperse away from the predator) by shy individuals, who were also more likely to utilize a refuge, had a longer latency to resume activity and were less likely to resume foraging than bold individuals. Larger conspecifics are the main predators of young-of-year smallmouth bass in the population from which subjects were collected. Predation pressure has been implicated as a cause of behavioral syndromes and the results of this study suggest that cannibalism in high density populations is sufficient to induce behavioural correlations.

Keywords: behavioural syndromes, personality, activity, antipredator behaviour, *Micropterus dolomieu*.

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DOI:10.1163/156853909X410784

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Introduction

The behaviour of an individual in one context can be highly correlated with its behaviour in other, unrelated contexts (Huntingford, 1976; Reichert & Hedrick, 1993; Wilson et al., 1993, 1994; Sih et al., 2004a,b). An individual might, for example, behave aggressively in competition for mates and also behave boldly while foraging in the presence of predators. Correlated behavioural characteristics across contexts have been known for quite some time, but their general ecological and evolutionary implications have only recently received attention (Gosling, 2001; Sih et al., 2004a,b). The suites of correlated characteristics are termed *syndromes* in evolutionary ecology and behavioural correlations across environmental contexts are known as *behavioural syndromes* (Sih et al., 2004a,b).

If the behaviour of an individual is correlated across multiple contexts, then its behaviour is likely to be beneficial in some, but not all, contexts (Sih et al., 2004a). Behavioural syndromes are consequently associated with fitness tradeoffs. For example, aggression could be beneficial, say, in a mate competition context, but boldness in a foraging context in the presence of a predator may not be. Likewise, a shy individual who engages in less risky behaviour may acquire fewer mates, but also experience a lower predation risk in the presence of a predator. These tradeoffs have important implications, as correlations have been observed between behaviours in many contexts, including foraging (Blumstein et al., 2004), dispersal (Dingemanse et al., 2003; Ribeiro et al., 2003; Rehage & Sih, 2004), antipredator behaviour (Riechert & Hedrick, 1993; Sih et al., 2003) and mate acquisition (Schulte-Hostedde & Millar, 2002). Thus, the measurement of individual behaviour in multiple contexts is essential to understand seemingly suboptimal behaviour, which may be part of a larger, constrained optimal life history strategy, where fitness tradeoffs vary temporally, spatially or ontogenetically (Bell & Stamps, 2004; Bell, 2005).

Behavioural syndrome studies provide insight into how individuals in a population may respond to dynamic environments. Behavioural syndromes in fishes are of special interest because many fishes grow over several orders of magnitude and changes of body size are often associated with shifts of environmental contexts (Breder & Rosen, 1966). Human water use and the inadvertent introduction of invasive species have also caused dramatic changes to many aquatic systems (Franssen et al., 2007). Studies of individual differences in behaviour in fishes have focused on individuals reared in
Behavioural syndromes in smallmouth bass

laboratories (Budaev et al., 1999a,b; Iguchi et al., 2001) or hatcheries (van Raaij et al., 1996; Sundström et al., 2004; Huntingford & Adams, 2005), and few behavioural syndrome studies have been conducted on subjects collected from natural populations (but see Wilson, 1998; Bell & Stamps, 2004; Bell, 2005; Brown et al., 2005). Studies of natural populations can provide information related to the occurrence and strength of behavioural syndromes and reveal the likely resilience of populations to environmental perturbations.

In this study, we used juvenile smallmouth bass (*Micropterus dolomieu*) collected from a minimally disturbed population and we measured the exploratory behaviour of individuals in an unfamiliar environment and their boldness in the presence of a simulated predator. The consistency of individual behaviour in these two contexts is likely to produce a fitness trade-off (Sih et al., 2004a,b). Exploratory behaviour familiarizes individuals with their environment, providing essential information on the location of food and shelter. Additionally, individuals who are familiar with their environment (i.e., are residents) are often more likely to be successful in competitive interactions (Krebs, 1982; Stamps, 1987; Sandell & Smith, 1991; Olsson & Shine, 2000). On the other hand, individuals who are bold in the presence of a predator may experience higher predation risk. For example, Bell and Sih (2007) found that sticklebacks (*Gasterosteus aculeatus*) that were bold in the presence of a simulated predator attack were more likely to be preyed upon when placed in a tank with a live predator.

Material and methods

Subjects and husbandry

Juvenile, young-of-year smallmouth bass (*Micropterus dolomieu*) were collected with a seine from Nebish Lake in late August 2006. Nebish Lake is a seepage lake located in the Northern Highland State Forest in north-central Wisconsin (46°04′N, 89°35′W), and it is one of five undeveloped research lakes studied extensively by the Wisconsin Department of Natural Resources (Raffetto et al., 1990; Hoff, 1995; Wiegmann & Baylis, 1995; Wiegmann et al., 1997, 2004). In addition to smallmouth bass, the lake supports yellow perch, *Perca flavescens*, blunt-nose minnows, *Pimephales notatus*, central mudminnows, *Umbra limi*, and hornyhead chubs, *Noemis biguttatus*.

Smallmouth bass were transported to Bowling Green State University, where they were maintained in environmental chambers on a 12:12
light/dark cycle. The chambers were held at a constant temperature of 12°C to reduce demands of husbandry. Subjects were held in groups of 12 individuals in 110-l aquaria and were fed black worms (*Lumbriculus variegatus*) through a 2.5 cm diameter plastic tube that released the worms near the bottom of the tank. Subjects were reared in these tanks for approximately six months prior to experiments. Three days prior to experimental manipulations subjects were removed from tanks in the environmental chamber and placed in groups of two or three individuals in 38-l holding tanks. They were transferred to an experimental room that had an ambient air temperature of 23°C. Subjects were food deprived over this 3-day acclimation period.

**Behavioural assays**

The behavior of subjects was quantified in two sequential sessions in a 110-l experimental tank, the bottom of which was divided into 18 equal-area sectors, with an acclimation chamber in one sector (Figure 1). The depth of the water in the experimental tank was 10 cm, which minimized vertical movements and allowed us to measure individual movement in two dimensions. Plastic aquarium plants were placed in each of the four corner sectors and a food dish was positioned between two of the plants. A 2.5 cm diameter plastic tube was used to deliver food into the dish in the second session.

**Exploratory behaviour session**

In the first session the exploratory behaviour of subjects in the (unfamiliar) experimental arena was quantified. A subject was chosen randomly from a holding tank and was placed in the acclimation chamber of the experimental

![Diagram of experimental arena](image)

**Figure 1.** Experimental arena. The experimental tank was a 110-l aquarium covered on the sides with black paperboard to ensure that the experimenter was not seen by subjects.
tank for 2 h. The door on the acclimation chamber was then opened and the time the subject took to exit the chamber was recorded. To quantify exploration we measured the number of sectors entered out of the possible 17 sectors and the total number of transitions made by subjects between sectors in the 3 min after a subject exited the acclimation chamber. A subject was defined to enter a sector when its body (snout to pectoral fin, inclusively) entered into a sector.

Behavioural responses to a simulated predator attack

In the second session a model avian predator was used to assess the boldness of subjects under predation risk. The distal end of a plastic replica of a heron beak was positioned 3 cm above the water surface and 2 cm to the side of the food dish. The second session was contiguous with the first session and was defined to begin 10 minutes after a subject exited the acclimation chamber, at which time ten worms were dispensed to the food dish. When a subject initiated feeding the replica heron beak was released to simulate an attack by a predator. The model beak penetrated 2 cm below the water surface and was immediately retracted.

In this session we measured four behavioural responses. The duration of continuous movement (one or more body lengths per 10 seconds) immediately after release of the model beak, referred to as the duration of active evasion, was measured. The location (open sector or sector with an aquarium plant) of a subject at the cessation of active evasion was also recorded. The duration of subsequent inactivity was measured as the time between the cessation of active evasion and resumed movement (as defined above), for thirty seconds. Finally, we measured whether or not a subject resumed foraging within 1 h of the simulated predator attack, when the session was ended. The total length (mm) of the subject was measured when the session was terminated. A total of 20 subjects was tested.

Data analysis

The behaviour of subjects within each session was summarized using a Principal Component Analysis (PCA) and a Spearman’s Rank Correlation \( r \) was used to compute the association between the principal component scores (Sokal & Rohlf, 1994). For our PCA, we utilized the eigenvalue greater than 1 rule to determine which components would be used in further analyses.
The benefit of compressing the data into component scores that summarize the behaviour of subjects within a context is that it avoids the increased risk of Type I error which occurs when multiple variables for each context are compared to one another individually (Bell, 2005, 2007). In addition, Spearman’s Rank Correlations were computed on individual variables to investigate individual differences in behavioural responses and to compare body length to principal component scores.

**Results**

**Within context behavioural analysis**

Individuals varied greatly in their behaviour within each of the sessions. In the first session of the experiment some individuals left the acclimation chamber in less than 1 min, while other individuals took over 45 min (\(\bar{X} \pm SE = 696 \pm 175\) s). In addition, some subjects were quite active and explored all 17 sectors in the experimental arena, while others explored as few as four sectors (\(\bar{X} \pm SE = 12.50 \pm 0.76\) sectors). In this session individuals made 7–55 sector transitions (\(\bar{X} \pm SE = 32.95 \pm 3.00\) transitions).

In the second session individuals spent 2–20 s in active evasion pursuant to the simulated predator attack (\(\bar{X} \pm SE = 10.40 \pm 1.16\) s). Six subjects ceased movement in an open sector and 14 subjects terminated movement in a sector occupied by an aquarium plant. Subjects subsequently resumed activity in as little as 2.5 min, but two individuals remained motionless for the entire hour after the simulated predatory attack (in subsequent analyses the latter two individuals received a conservative maximum resumed activity score of 1 h). Only 9 of the 20 subjects resumed foraging in the hour following the simulated predatory attack.

**Principal component scores**

The principal component scores within each context are summarized in Table 1. Only the first component score within each context had an eigenvalue equal to or larger than 1. In the first context the latency to leave the acclimation chamber loaded positively on the first component score while the subsequent number of sectors explored by subjects and the number of sector transitions by subjects loaded negatively (72.8% of variance explained). High positive values of this component score correspond to relatively inac-
Table 1. Results of principal component analysis on behaviour within each context.

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Loading</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Exploratory behaviour</strong></td>
<td></td>
</tr>
<tr>
<td>Latency to leave shelter</td>
<td>0.520</td>
</tr>
<tr>
<td>Number of sectors explored</td>
<td>-0.636</td>
</tr>
<tr>
<td>Total sector transitions</td>
<td>-0.570</td>
</tr>
<tr>
<td>Cumulative variance explained</td>
<td>72.8%</td>
</tr>
<tr>
<td><strong>Response to simulated predator attack</strong></td>
<td></td>
</tr>
<tr>
<td>Duration of active evasion</td>
<td>0.447</td>
</tr>
<tr>
<td>Cessation of motion in sector without a plant</td>
<td>-0.408</td>
</tr>
<tr>
<td>Time to resume activity</td>
<td>0.621</td>
</tr>
<tr>
<td>Resumption of foraging</td>
<td>-0.498</td>
</tr>
<tr>
<td>Cumulative variance explained</td>
<td>47.1%</td>
</tr>
</tbody>
</table>

Positive (negative) loadings correspond to a positive (negative) association between high values of a measured variable and high (low) values of principle component scores.

tive, shy subjects, who had long latencies to leave the acclimation chamber and explored little of the test arena.

In the second context the duration of active evasion and the subsequent period of inactivity loaded positively on the first component score while cessation of movement in an open sector, rather than in a sector with an aquarium plant, and resumed foraging loaded negatively (47.1% of variance explained). A high positive value on this component score consequently corresponds to shy subjects who had long durations of active evasion (presumably to disperse from the model predator), were more likely to cease active evasion in a sector with an aquarium plant and subsequently remain inactive for a long period of time, and who were unlikely to resume foraging within the hour after the simulated predator attack.

Behavioral correlations across contexts

The principal component scores for individuals in the exploratory behaviour session were positively correlated to the principal component scores in the behavioural responses to a simulated predator attack session ($r = 0.658; p = 0.002$; Figure 2). These results indicate that subjects who engaged in exploratory behavior in the unfamiliar environment of the test arena also tended to behave boldly after the simulated predator attack in the second
Figure 2. The relationship between the exploratory behavior of subjects in the unfamiliar test arena in the first session of the experiment and their responses to a simulated predator attack in the second session. Axes are the first principal component scores within each session. High values on the $x$-axis correspond to individuals who engaged in minimal exploratory behavior while high values on the $y$-axis correspond to shy individuals. A Spearman’s Rank Correlation reveals a significant correlation between scores across contexts ($r = 0.658; p = 0.002$).

There was no significant correlation between the body length of subjects ($\bar{X} \pm \text{SE} = 71.5 \pm 2.1 \text{ mm}$) and their principal component scores in either the first session ($r = -0.269; p = 0.251$) or the second session ($r = -0.311; p = 0.182$).

The comparisons of measured behaviour in the two contexts also revealed behavioural consistency across contexts (Table 2). For example, the latency to leave the acclimation chamber in the first session was positively correlated with the duration of active evasion and the subsequent period of inactivity by subjects in the second session. Latency to leave the acclimation chamber in the first session was also negatively correlated with the likelihood that a subject ceased active evasion in an open sector (rather than in a sector occupied by an aquarium plant) and the likelihood that an individual resumed foraging in the hour following the simulated predator attack.
Table 2. Spearman’s Rank Correlation coefficients for comparisons of individual variables across contexts.

<table>
<thead>
<tr>
<th></th>
<th>First session</th>
<th>Second session</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Duration of active evasion</td>
<td>Cessation of motion in sector without a plant</td>
</tr>
<tr>
<td>Latency to leave shelter</td>
<td>0.516 (0.020)</td>
<td>−0.530 (0.016)</td>
</tr>
<tr>
<td>Number of sectors explored</td>
<td>−0.540 (0.014)</td>
<td>0.305 (0.191)</td>
</tr>
<tr>
<td>Total sector transitions</td>
<td>−0.577 (0.008)</td>
<td>0.456 (0.043)</td>
</tr>
</tbody>
</table>

*p* values are given in parentheses.

**Discussion**

In this study, we compared the exploratory behaviour of juvenile smallmouth bass in a novel environment with their responses to a simulated predator attack and found evidence of a behavioural syndrome: subjects who actively explored the unfamiliar test arena exhibited more risky behaviour pursuant to the simulated attack by a predator. In particular, subjects who exited the acclimation chamber rapidly and explored the test arena had shorter durations of active evasion, were more likely to cease motion in an open sector of the arena (rather than near an aquarium plant), were quick to subsequently resume activity and were more likely to resume foraging within an hour of the attack by the model predator.

The observed behavioral syndrome suggests that juvenile smallmouth bass from Nebish Lake make important fitness tradeoffs. Low levels of exploratory behavior and long periods of inactivity following a predator attack probably reduce the risk of predation, but also presumably reduce encounters with prey and the opportunity to obtain information related to other important resources, such as shelter (Petranka & Sih, 1987; Verbeek et al., 1994; Maurer & Sih, 1996). The results of this study also suggest that bold individuals adopt a different anti-predator strategy than shy individuals. Shy individuals, who take longer to enter a novel environment and engage in little exploratory behaviour, are likely to seek shelter in risky situations and are likely to disperse farther from a value resource to avoid predators.

The results of recent studies indicate that predation pressure may play an important role in whether or not a population exhibits behavioral syndromes...
(Bell, 2005; Bell & Sih, 2007; Dingemanse et al., 2007). For example, studies of sticklebacks reveal that behavioural syndromes occur more often in populations that experience predation pressure than in populations devoid of predators (Bell, 2005; Dingemanse et al., 2007), and in an experimental study Bell and Sih (2007) found that predation pressure induces behavioural syndromes.

In this study we observed a behavioral syndrome in juvenile smallmouth bass from a population in which the main predation pressure is in the form of cannibalism. The pristine water quality of Nebish Lake and the abundant food resources support a robust population with an average density of about 40 adult smallmouth bass per hectare, a density considerably higher than most of the other smallmouth bass populations monitored in northern Wisconsin lakes (Engel et al., 1999). Escanaba Lake, a research lake adjacent to Nebish Lake, for example, supported only 3.5 adult smallmouth bass per hectare in 2004 (Newman et al., 2005). The results of this study suggest that predation pressure by conspecifics in high density populations may be sufficient to induce behavioural syndromes.

Acknowledgements

We thank A.M. Bell and A. Sih for helpful discussion, T. Holmes for editorial comments, A.R. Johnson and C.J. Winslow for assistance with collecting smallmouth bass and the University of Wisconsin Trout Lake Station for providing logistical support while we were in the field.

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