Personalities in a crowd: What shapes the behaviour of Eurasian perch and other shoaling fishes?

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Abstract  Lately, there has been an increasing interest in intraspecific variation in behaviour, and numerous studies on personality have been performed in a variety of animals, including several fish species. Individuals have been divided into coping style categories or arranged along a behaviour gradient, such as the bold/shy continuum. However, many fish species live in groups, and the social environment can influence the behaviour of an animal in different ways. There may be conflicts within groups due to competition for resources, and dominance hierarchies are commonly found. On the other hand, there are many benefits of consensus decision-making within the group. Conformity of behaviour is probably adaptive, due to the benefit of public information on, for example, food resources and predation risk. Accordingly, studies of fish shoals have found evidence of consensus decision-making. Furthermore, factors in the environment, such as predation risk would also influence the behaviour expressed. To be able to understand behaviour patterns in a group of fish, it is necessary to consider the variation of individual characteristics, and how the group, as well as other environmental factors, affects the behaviour of individuals. Here, I will review studies on different aspects of personality within a social context in fish, with a special emphasis on the Eurasian perch Perca fluviatilis [Current Zoology 58 (1): 35–44, 2012].

Keywords Perca fluviatilis, Boldness, Group influence, Behavioural syndromes, Consensus, Predation risk

1 Introduction

When observing the behaviour of animals, it is often obvious that not all individuals within a species react in the same way when exposed to the same type of stimulus, even if they are of the same age, sex, and from the same background. Studies of this intraspecific variation in behaviour have been performed on a variety of animals (reviewed in Sih et al., 2004; Réale et al., 2007), and this phenomenon has been referred to with several different terms, such as personality, temperament, coping style, and behavioural syndromes. Personality and temperament are terms that cover several components in an individual’s behaviour, such as boldness, sociability and aggressiveness. To consider a behaviour pattern to be caused by an individual personality trait, it should be possible to find a consistency within context (Réale et al., 2007). In accordance with observed behaviour, individuals have been divided into coping style categories (Koolhaas et al., 1999) or been arranged along a behaviour gradient, such as the bold/shy continuum (Wilson et al., 1993). Behavioural syndromes can be seen as subsets of personality classifications, and are defined as correlations, within a species/population, between different types of behaviour or between behaviour in different contexts (Sih et al., 2004; Bell, 2007). The variance in personality probably has a complex physiological and hormonal foundation (Koolhaas et al., 1999). Neuroendocrine characteristics have earlier been found to be linked to aggression and dominance in fish, with individual production of stress hormones affecting dominant-subordinate relationships in rainbow trout, Oncorhynchus mykiss (Pottinger and Carrick, 2001). How variation in personality can be maintained within a population, and whether fitness of different personality types can be affected by environmental factors are related questions currently discussed (e.g. Smith and Blumstein, 2008; Adriaenssens and Johnson, 2011; Culleter and Brown, 2011). Other studies address how the existence of fish personalities can be applied in the fields of fisheries management (Conrad et al., 2011) and aquaculture (e.g. Øverli et al., 2006; Mas-Munoz et al., 2011). Studies on personality are usually performed on individuals in solitude (e.g. Verbeek et al., 1994; Sneddon, 2003; Bell, 2005; Dingemanse et al., 2007), to avoid the confounding effects of social interactions and personality. However, when studying the individual behaviour...
of animals that naturally live in groups the question arises – how much of the observed behaviour in a natural situation is caused by an individual’s personality traits and how much is due to the influence of the group? Individual differences in behaviour has been suggested both to increase (by self-organisation, Hemelrijk and Wantia, 2005) and to decrease (by consensus decisions, Sumpter et al., 2008), as group size increases. Studies on animal behaviour that are looking at social interactions are numerous (reviewed in Krause and Ruxton, 2002). In fish, the occurrence of dominance hierarchies and their effect on food competition has been particularly well studied (Brännäs et al., 2001; Leblond and Reebs, 2006). However, only a few studies have looked at the combined effect of individual personality and group interactions [see Magnhagen and Staffan, 2005; Dyer et al., 2008 (fish); Sih and Watters, 2005 (water striders); review by Webster and Ward, 2011]. To increase our understanding of behaviour patterns in animal groups, it is necessary to consider both the variation of individual characteristics within groups and how the group composition affects the behaviour of individuals.

In this review, I will look at studies on intraspecific variation in the behaviour of fishes, and discuss how the social context will affect the behaviour of an individual, as well as how individuals may influence the general behaviour of the group. The literature around the topics personality and social behaviour is currently growing fast, and for practical reasons I will mainly refer to studies on fish, with a few exceptions. I will base the review around studies on the Eurasian perch *Perca fluviatilis*.

Specific questions addressed are:

- Why and how should individual behaviour be studied in groups when dealing with social animals?
- What kind of behaviour variation within groups has been demonstrated?
- How can the group influence individual behaviour, and are all individuals equally affected?
- How are environmental factors influencing individual and social behaviour?
- Are consistent behaviour patterns due to inherited traits?
- Is there a contradiction or a connection between personality and phenotypic plasticity?

## 2 The Eurasian Perch

Eurasian perch is a common freshwater species with ontogenetic niche shifts that lives in big shoals during the first years of life, but in smaller groups after this period (Persson, 1988). It generally changes its diet with increasing size from plankton to macrobenthos and finally fish. As a piscivore, it can be an important predator on the young perch (Treasurer, 1989; Persson et al., 2004). Depending on size structure of the population, predation pressure from cannibalism varies among lakes (Magnhagen, 2006), making perch a suitable species in which to study the effect of population structure on the behaviour of potential prey fish.

Together with my colleagues I have used the Eurasian perch as a model organism to look at consistency of individual variation in boldness and the effect of the group on behaviour (see e.g. Westerberg et al., 2004; Magnhagen and Staffan, 2005; Magnhagen and Borcherding, 2008; Magnhagen and Bunnefeld, 2009; Hellström and Magnhagen, 2011). In general, we have looked at individual trade-offs between foraging in a risky area (open, near a piscivorous perch behind a net screen) and stay in shelter (vegetation away from the piscivore). Individuals spending more time in the open and feed more on the bloodworms on the bottom of the aquarium are considered bolder than those that spend more time in the vegetation where food is not available. Specific questions that we addressed are how individual behaviour varies within groups, the correlation of different behaviours, conformity to the group, and the effect of experience.

## 3 Studying Behaviour in Groups

Many fishes live in groups, from small, loosely connected shoals to highly synchronized schools of thousands of individuals (see e.g. Pitcher and Parish, 1993). Some suggested advantages with group living are protection against predation, due to dilution and confusion effects, and the utilization of the information from other individuals on predation risk and food resources (e.g. Pitcher and Parrish, 1993; Krause and Ruxton, 2002). Social information transfer may lead to a more efficient decision-making in shoals (Ward et al., 2011). These benefits are accompanied with costs as competition for food and other resources, and perhaps also the attraction of predators to big groups of fish. Also, individual behaviour within a group is affected by social influences (Hemelrijk and Wantia, 2005; Sumpter et al., 2008; Conradt et al., 2009).

The difference between individual behaviour in solitude and in a social context has been considered in only a few fish studies (Reebs, 2000; Webster and Hart, 2006; Webster et al., 2007; Magnhagen and Bunnefeld, 2009;
see also van Oers et al., 2005 on birds). In a study comparing growth rate and food efficiency in perch of different group sizes, growth rate was lower in single perch than in groups, despite a higher food intake (Strand et al., 2007). Also, oxygen consumption was higher in perch kept in solitude compared to those kept in groups (Schleuter et al., 2007). The presence of conspecifics seems to reduce the energetic costs, maybe through a decrease in stress levels. This assumption was supported by a behaviour study where one-year-old perch were bolder when observed in a group of four fish than when kept alone (Magnhagen and Bunnefeld, 2009). A similar result was obtained for the three-spined stickleback *Gasterosteus aculeatus* (Webster et al., 2007). In that study, fish were more active and resumed foraging more rapidly after a simulated predator attack when they were in groups relative to when tested alone. These results make it relevant to use groups of fish rather than individuals when studying behaviour of social fishes.

However, when studying individual variation of animals in groups, there is a problem with the interdependence of the data. It is therefore important to adjust for the effect of the group. Sometimes focal individuals are used, as when the response to a conspecific dummy was investigated in sticklebacks within different sized groups (Ward et al., 2008). Here only one fish in each group were chosen as a study object. Individuals within a group can also be ranked according to some specific measure, as the amount of food eaten relative to the others in a group of perch (Westerberg et al., 2004). These methods, although sometimes suitable, does not take into account that the individual behaviour may be affected by group composition. Alternatively, relative values, as deviation from the group mean can be used (Leblond and Reeb, 2006; Magnhagen, 2007). These residual values show how the individual behave in relation to its group members, but the result can vary depending on group composition.

An alternative method of dealing with the problem is the use of mixed effects models, where interdependency within groups can be taken into account, and the effects of the different factors that form an animal’s behaviour can be estimated. With a hierarchical nested design, where the individuals are nested into group, the problem with pseudoreplication is avoided. Also, from these mixed effects models, individual scores (BLUPs, i.e. best linear unbiased predictors) can be extracted, and used as behavioural measures, adjusted for the group influence (see e.g. Boon et al., 2007; Dingemanse et al., 2007). In aquarium studies, Dingemanse et al. (2007) categorized five types of behaviour in twelve populations of sticklebacks. They used BLUPs extracted from models analysing the different behaviour categories separately, with individuals nested within populations. Behavioural syndromes, defined as correlations between BLUPs, were found in predator-sympatric populations to a higher degree than in populations without experience of predation.

It is also possible to tease apart individual personality traits and the influence of the group by looking at variance components in the mixed effects models (Pinheiro and Bates, 2000). The use of variance components has lately been recognized as a successful tool to evaluate the impact of confounding factors, such as heritability, phenotypic variance, and random effects, in studies of ecology and behaviour (e.g. Bunnefeld et al., 2009; Dingemanse et al., 2009). In this way the individual variation within the groups can be compared with the variation among groups, and the consistency within individuals can be estimated (Pinheiro and Bates, 2000; Börger et al., 2006).

## 4 Individual Variation within Groups

Individual behaviour differences within a shoal of fish are often connected with dominance hierarchies. Dominant fish are often more aggressive, active, and bold, as in groups of male rainbowfish *Melanotaenia duboulayi* (Colleter and Brown, 2011) Thus, some individuals within a group may suppress the foraging rate of others (see e.g. Brännäs et al., 2001), or act as leaders, determining movement patterns and directions (Reebs, 2000; Leblond and Reeb, 2006). In the golden shiner *Notemigonus crysoleucas* tested in groups, shoal leaders arose, and these individuals also had a tendency to be more explorative (Leblond and Reeb, 2006). Similarly, in three-spined sticklebacks there was a correlation between boldness and initiative, with bold fish showing stronger tendencies to take front positions in a shoal than shy conspecifics (Ward et al., 2004). Bold sticklebacks were acting as leaders, and shy fish followed the bold fish’s movements (Harcourt et al., 2009). Bold individuals may thus influence the behaviour of the whole group.

In one of our first studies on individual variation in perch behaviour, we used young-of-the-year fish, and ranked individuals in groups of four according to mean food intake over a study of ten days. Individuals with the highest total food intake had consistently the highest daily feeding rate, and vice versa (Fig. 1, Westerberg et al., 2004). This could depend on differences in competi-
tive ability, but we also found that all individuals in the group, except the highest ranked fish, increased the time hiding in the vegetation in the presence of a predator in comparison with in its absence. Therefore, it seemed like the fish that had the highest rank had both most to eat and was the boldest individual in its group.

Fig. 1 Number of prey attacks (mean ± 95% CI) performed by perch ranked according to averaged food intake over a period of ten days (circles show individuals with highest mean intake, triangles those with the lowest mean intake, etc.), in aquarium experiments with twelve groups of four young-of-the-year perch
Data from Westerberg et al. (2004).

Within context, the variation in the behaviour of perch seems consistent, as repeated measures of time in the open area, as well as number of prey eaten are always highly correlated, thus supporting the notion of consistent individual differences within groups (Fig. 2, data from Magnhagen and Borcherding, 2008). The correlation between behaviour in different contexts has also been studied (Magnhagen, 2007). The same individuals were tested for boldness in the standard setup, and then explorative behaviour was investigated in another test, where time to enter a passage to an unknown area was a measure of explorative tendency. There was a correlation between the two parameters, but only when adjusting for the behaviour of the other fish in the group, either using the differences from the mean of the other group members (Magnhagen, 2007) or extracting BLUPs from a linear mixed effects model with individual behaviour measures nested within groups (Fig. 3). Thus, behavioural syndromes, defined as correlations between different behaviours can be distinguished in individual perch, even if they are affected by the others in the group.

Fig. 2 Correlations between individual measures of percentage of time spent in the open area and percentage of time feeding during first and third run in repeated observations on risk-taking behaviour in young-of-the-year perch
Correlations between second run and the other runs are also significant (P<0.001), but not presented here. Data from Magnhagen and Borcherding (2008).

Fig. 3 Correlation between time spent in the open area and latency to enter novel area in two separate aquarium studies
Data is presented as BLUPs from linear mixed-effect models, with groups and individuals, nested in groups, as random factors. Data from Magnhagen (2007).
5 Effects of the Group on Individual Behaviour

There may be several ways that the group can affect the behaviour of individuals. In fishes where dominance hierarchies occur, the effect depends on the individual rank, with aggressive individuals suppressing others, thus influencing the scope of activities for subordinate shoal members (Brännäs et al., 2001). This indicates that there is a conflict within the group; in other cases the group association leads to benefits, via the possibility to follow and/or imitate shoal mates, and to receive information. There are many benefits of consensus decision-making within groups, and examples can be found in a variety of taxa (Sumpter and Pratt, 2009). In our perch studies, even though differences in boldness (including time spent in a risky habitat, latency to start feeding, etc.) within groups are consistent, estimates of variance components show that the variation in behaviour among groups often is bigger than the variation within groups (Fig. 4, Magnhagen and Bunnefeld, 2009). This indicates that the perch within each group conform to each other to some extent (but this may differ among populations, see below). Conformity of behaviour is probably often adaptive, due to the benefit of public information on, for example, food resources and predation risk (Krause and Ruxton, 2002). Accordingly, several studies on fish shoals have recently found evidence of consensus decision-making within the group (e.g. Sumpter et al., 2008; Ward et al., 2008). Three-spined sticklebacks used public information when choosing among feeding areas and were shown to prioritise social conformity over the use of private information (Webster and Hart, 2006). In guppies Poecilia reticulata conformity to the group depended on group size and context (Day et al., 2001). Predation risk may also select for conformity when individual information gathering leads to high costs. European minnows Phoxinus phoxinus used public information under simulated predation risk, while private information was used in low risk situations (Webster and Laland, 2008).

An interesting study by Dyer et al. (2008) showed that the composition of personalities in a group of guppies influenced the foraging success of all its individual members, and a mix of behavioural types performed better than all-bold or all-shy groups. Also, the average personality composition of populations of mosquitofish Gambusia affinis affected dispersal and settlement decisions in individuals, regardless of own personality (Cote et al., 2011). We tested individual perch in different group compositions (Magnhagen and Staffan, 2005). They were first tested for boldness in random groups, and then sorted into groups with the same boldness scores in the first test. Previously shy individuals increased time in the open when grouped only with other shy individuals, but bold individuals decreased time in the open. This could be interpreted as an increase in competition to access to the open area in the bold groups and a relaxation of competition in the shy groups. The shy fish ate more in the all-shy treatment than in the earlier mixed treatment, supporting the competition explanation. However, the results must also take into account habituation to the experimental set-up, since the group of only bold fish depleted the food resource quicker and then returned to the vegetation. Shy fish, on the other hand, have been found to increase risk taking also with habituation and change of environment (Magnhagen and Bunnefeld, 2009).

An individual fish thus seems to be influenced by the company it keeps and may adjust its behaviour to conform to the crowd. The question is, are all individuals equally affected by the group, or can we see variation also in this aspect of behaviour?

6 Correlations between Boldness and Sociability

A negative correlation between the degree of boldness and social tendency has been found in several fish species. Bold individuals often act more independently than shy ones that are more likely to cooperate (Krause et al., 2008). Bold three-spined sticklebacks interacted
less with other individuals within a group compared to shy fish (Pike et al., 2008). The shy fish interacted more often, but with fewer individuals than did the bold ones. The ocellated wrasse *Symphodus ocellatus* show a large variation in schooling tendencies (Budaev, 1997). When placed in a novel environment, solitary individuals were bolder and more active compared to conspecifics that had been observed schooling. Similarly, boldness and sociability were correlated traits in the invasive mosquitofish *Gambusia affinis* (Cote et al., 2010). Interestingly, the bold and unsocial individuals were found to have a higher tendency to disperse (but see also Cote et al., 2011). Also in Trinidad killifish *Rivulus hartii* bold individuals dispersed further than shyer ones (Fraser et al., 2001). It may have ecological implications if a population of an invasive species has another personality distribution in newly occupied areas than in the original one. If bold invaders also are more aggressive they can have a large impact on the new environment (Cote et al., 2010).

### 7 Effect of Environment on Social Behaviour

One explanation for schooling in fish is the protection against predation. This was supported by an early study on the Trinidad guppy comparing streams with different predation risk (Seghers, 1974). In populations living with high density of large piscivores schooling was more developed, with more cohesive groups, than in populations with only smaller piscivores. When predation risk was low, schooling behaviour was even absent. Thus, the environment can influence the social behaviour of fish, either through natural selection or by phenotypic response to certain key factors, such as density of predators. This was also found in the European minnow, in which populations that occur sympatrically with pike *Esox lucius* form more cohesive schools than populations living in areas without pike (Magurran, 1990). Furthermore, a stronger tendency to school was found in marine three-spined sticklebacks than in freshwater benthic conspecifics, and there were also differential preferences for social vs. non-social (i.e. shelter) options between the two types, with marine sticklebacks being more social (Wark et al., 2011). The schooling behaviour was found to be inherited, and was similar among individuals within a population even when they had been kept with fish from other populations and with other schooling tendencies (Wark et al., 2011).

Perch live in a wide range of habitats, and the extent of predation pressure may differ among populations. Depending on population density and size structure, cannibalism can be severe (Treasurer, 1989; Persson et al., 2004). In a study of four lakes, risk-taking behaviour in aquarium studies was correlated with risk of cannibalism (Magnhagen, 2006). Two of the lakes, Ångersjön and Fisksjön, show a big difference in the density of potential cannibals (Magnhagen, 2006). The perch from these lakes repeatedly show significant differences in risk-taking behaviour, with young-of-the-year perch from Ångersjön being consistently bolder than those from Fisksjön (Magnhagen, 2006; Magnhagen and Borcherding, 2008; Hellström and Magnhagen, 2011). When estimating variance components from mixed-effects models, testing the nested random effects of group, individual and repeated run on boldness, separately for the two lakes and for two age classes (young-of-the-year and one-year-old fish), some interesting patterns were found (Table 1, re-analyzed data from Magnhagen and Borcherding, 2008). In Ångersjön, differences among individuals within groups explained the variance in boldness score to a higher degree that the differences among groups, indicating a low degree of conformity within the group. In Fisksjön, on the other hand, there was almost no variance among individuals within groups. The same pattern was found in both age classes (Table 1). These results may be explained by a difference

### Table 1
The percentage of total variance of the boldness score PC1 explained by the nesting factors within individual (repeated runs), among individuals, among groups and the residual variance of the random effects of mixed effect models, for 0+ and 1+ perch from the lakes Ångersjön and Fisksjön, tested separately.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Age</th>
<th>Among groups</th>
<th>Among individuals</th>
<th>Within individual</th>
<th>Residual</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ångersjön</td>
<td>0+</td>
<td>3.6</td>
<td>10.7</td>
<td>76.9</td>
<td>8.7</td>
</tr>
<tr>
<td></td>
<td>1+</td>
<td>25.4</td>
<td>32.8</td>
<td>34.7</td>
<td>7.1</td>
</tr>
<tr>
<td>Fisksjön</td>
<td>0+</td>
<td>20.9</td>
<td>&lt;0.001</td>
<td>79.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>1+</td>
<td>51.1</td>
<td>&lt;0.001</td>
<td>48.8</td>
<td>0.0</td>
</tr>
</tbody>
</table>

PC1 is produced by a principal component analyses including time in the open, latency to enter open area, latency to start feeding, and number of changes between habitats. Eight groups were tested for each category. Data from Magnhagen and Borcherding 2008.
in shoaling behaviour and cohesiveness, depending on the experience of predation. More directed studies, preferentially including more populations, must be performed to establish if this is a general pattern. It would also be interesting to see whether shoaling behaviour is an inherited trait selected for by predation pressure.

8 Heritability of Boldness

We have found consistent differences in behaviour between the populations in our two test lakes, Ångersjön and Fisksjön, regarding individual boldness and conformity within groups. With Fisksjön having a higher density of potential cannibals than Ångersjön, this may depend on differential selection in the two lakes due to differences in predation pressure on the young stages. On the other hand, it may simply be an effect of phenotypic response to the environment. There are studies on other fish species with evidence in both directions. Populations of a poeciliid fish, the Panamanian bishop Brachyraphis episcope show behavioural syndromes associated with predation pressure (Archard and Braithwaite, 2011). In contrast to the perch, fish from high-predation populations are bolder, more explorative and more active than those from low-predation populations, but there is also individual variation within populations. When raised in the laboratory, the offspring showed a behaviour similar to their wild parents, suggesting that boldness is an inherited trait (Brown et al., 2007). However, simulated attacks in the tanks also influenced the behaviour, increasing boldness in both high- and low-predation populations. Thus, experience also plays a role in the development of behaviour patterns. In the guppy, the heritability of schooling behaviour that differs in populations with different predation risks have been shown over several generations in the laboratory (e.g. Seghers, 1974; Breden et al., 1987). Of interest for the topic of this review, individual response to predators can be also affected by the group to which the individual guppy is associated (Kelley et al., 2003). Guppies from low-predation sites improved their anti-predator response when exposed to a predator model in the company of a high-predation group compared to a control with guppy from their own population. That study also connects to the dynamic field of social learning (review on fish by Brown and Laland, 2003), which is beyond the scope of the present review.

Perch from our two study lakes were hatched and raised in ponds without piscivores (Hellström and Magnhagen, 2011). After the first growth season boldness was tested in the standard setup, and the behaviour of the pond-raised fish was compared with wild-caught fish from the same lakes and cohorts. The wild perch showed the same difference in boldness as in previous studies (e.g. Magnhagen and Borcherding, 2008). In contrast, the pond-raised perch from the two populations showed very similar behaviour, and were as risk-prone as perch from the boldest wild population, that is, the one with low predation pressure (Hellström and Magnhagen, 2011). Thus, their behaviour seemed to be influenced by experience to a large extent.

The studies presented in this section show diverging results concerning the heritability of boldness. Whatever proximate and ultimate mechanisms that underlie the variation in behaviour; the environment, including group association and predation risk, obviously has the ability to shape the behaviour of an individual fish. The occurrence of both personality and plasticity may seem like a contradiction. Thus, the interaction between personality and ability to show phenotypic plasticity is an exciting field for further exploring (Dingemanse et al., 2010).

9 Personality versus Phenotypic Plasticity

Whether fixed or flexible behaviour is the most optimal, has been discussed elsewhere (Wilson et al., 1994; Dingemanse et al., 2010). The costs and benefits of being bold or shy probably vary among different environments, but there may also be a cost of producing or maintaining phenotypic plasticity (DeWitt et al., 1998). Wilson et al. (1994) suggested that in a constant environment it will be beneficial to be a specialist, that is, to stick to a fixed response to risk, rather than being a generalist and switch between being risk-prone and risk-averse. However, the ability to be phenotypically plastic may differ between individuals. There are some indications that individuals with different personalities also show different degree of plasticity (Dingemanse et al., 2010). Briffa et al. (2008) suggested that differences among individuals in cognitive ability, sensory acuity, and physiology could lead to differences in behavioural plasticity. They looked at the balance between behavioural plasticity and personality by comparing startle responses in the hermit crab Pagurus bernhardus exposed to different cues of predation risk. Their results showed evidence of plasticity but the consistency of individual behaviour was stronger (Briffa et al., 2008). In some fish species plasticity seems to vary with per-
sonality, with shy individuals being more plastic than bold ones. In the three-spined stickleback, shy fish were more variable in their behaviour than bold fish, having a greater range of reaction times when responding to foraging tasks (Harcourt et al., 2010). Shy perch seem to be more flexible than bold ones, since they change their behaviour more with habituation (e.g. Magnhagen and Staffan, 2005) and predation risk (Westerberg et al., 2004). Also in rainbow trout a difference in flexibility between fish of different personalizations was found. In this species, two separate strains have been selected according to high (HR) and low (LR) post stress plasma cortisol levels, also showing differences in behaviour and defined as proactive (low stress response or bold) and reactive (high stress response or shy) (Øverli et al., 2002). When changing the location of the food, proactive LR fish were markedly slower than reactive HR fish in altering their food seeking behaviour in response to relocated food (Ruiz-Gomez et al., 2011). The bold fish even swam right over the new feeding location, seemingly without noticing the food, and instead went directly to the old food source. In contrast, the shy fish found the food almost immediately after the change (Øverli et al., 2002). In juvenile convict cichlids Amatitlania nigrofasciata exploratory tendency was correlated with response to predation risk, with longer reaction times in fish that were fast to explore a novel environment (Jones and Godin, 2010). The authors suggested that the result could depend on individual trade-offs between foraging and anti-predator vigilance. If there is a general connection between boldness and plasticity, with shy individuals being more flexible than bold ones, this could perhaps be one explanation to why shy fish are more cooperative and conform to the group, as discussed in an earlier section.

10 Concluding Remarks

The numerous studies that have looked at behavioural variation within fish species and populations have found evidence that discrete personalizations occur, and that group association affects individual behaviour. It is also clear that the behaviour observed is formed by a whole range of different conditions. Different behavioural traits have been found to be related, for example, bold fish seem to be less sociable than shy ones, and shy fish show a higher degree of flexibility, which may affect their performance in groups. These findings are supported by studies on a variety of fish species. Here I recapitulate some of these conditions using our model fish, the perch. In a standardised aquarium test of boldness, measured as risk-taking behaviour, we have found that individuals show consistent behaviour over time and across contexts. The individuals are also much influenced by the group in which they occur, and seem to conform to an average group performance. However, the degree of conformation seems to depend on personal and origin. The environment in which the perch lives can affect its behavioural development, for example, by giving cues about the risk of being caught by a predator. Experience seems to influence behaviour decisions of the fish. Thus, to understand the behaviour patterns within a group of fish, it is necessary to consider the variation of individual characteristics, and how the group, as well as other environmental factors, affect the behaviour of individuals.

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