Phenotypic and social effects on behavioural trade-offs in Eurasian perch

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Abstract

Trading between conflicting demands is a fundamental part in how animals interact with its environment and social surrounding. Knowledge of what factors shaping trade-off decisions is central in our understanding of animal adaptation and ecology. This thesis summarizes a series of behavioural experiments investigating how animals compromise behaviours depending on environmental background and context. The focus is on within- and between-population variation in risk-taking and social trade-offs in young of the year and one year old Eurasian perch. Perch behaviour was quantified by observational studies in aquaria, using standardized assays that captured perch boldness and sociability. Perch from different predation backgrounds were contrasted in common garden experiments, as well as in multi-year inter-population comparisons, to study influence of predation experience on risk-taking phenotype. Results demonstrate predation as an important factor underlying how perch balance risk. Variation in risk-taking phenotype could to a large extent be explained by individual differences in experience of predation, rather than by fixed inherited responses caused by divergent selection. Experience of predation had long lasting effects on perch boldness, but perch were also able to quickly adjust phenotype in response to current conditions, indicating temporal flexibility in how experience shape behaviour. Social context influenced behaviour, with fish being bolder in larger group, and showing higher behavioural conformity. Occurrence of consistent individual variation in risk-taking and social behaviour could be established, confirming the existence of a personality dimension in perch behaviour. The thesis concludes that variation in how perch trade-off conflicting behaviours exists at multiple levels, from population to individual. Behavioural plasticity, even in strongly fitness related traits, is evident, although potential behavioural constraints in the form of consistent individuality is also present.

Keywords: boldness, adaptation, predation, sociability, risk, experience, *Perca fluviatilis*

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Dedication

To my family

It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is most adaptable to change

Charles Darwin

I know the human being and fish can co-exist peacefully

George W. Bush

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hellström, G., Magnhagen, C. 2011. The influence of experience on risk taking. Results from a common-garden experiment on populations of Eurasian perch. Behavioral Ecology and Sociobiology, 10:1917-1926

II Magnhagen, C., Hellström, G., Borcherding, J., Heynen, M. Boldness in two perch populations – long-term differences and the effect of predation pressure. Journal of Animal Ecology, in press

III Hellström, G., Magnhagen, C. 2011. Balancing past and present – how experience influence boldness over time in Eurasian perch. Submitted manuscript

IV Hellström, G., Heynen, M. Oosten J. E., Borcherding, J., Magnhagen, C. 2011. The effect of group size on risk taking and social conformity in Eurasian perch. Ecology of Freshwater Fish, 20: 499–502

V Hellström, G., Heynen, M., Borcherding, J., Magnhagen, C. Influence of context and personality on group-size preference in Eurasian perch. Submitted manuscript.

Papers I, II and IV are reproduced with the permission of the publishers.

The contribution of Gustav Hellström to the papers included in this thesis was as follows:

I Designed and planned jointly with C. Magnhagen, executed behavioural experiments, processed statistical data, and compiled the manuscript.

II Designed and planned jointly with C. Magnhagen, M. Heynen and J. Borcherding. Some involvement in behavioural experiments, processing of data and compilation of manuscript.

III Designed and planned jointly with C. Magnhagen, executed behavioural experiments, processed statistical data, and compiled the manuscript.

IV Designed and planned jointly with C. Magnhagen, M. Heynen, J. Oosten and J. Borcherding, executed behavioural experiments, processed statistical data, and compiled the manuscript.

V Designed and planned jointly with C. Magnhagen, M. Heynen and J. Borcherding, executed behavioural experiments, processed statistical data, and compiled the manuscript.

Prologue

I had bought new fish to my aquarium, and under the expectant gaze from my six year old niece, I carefully poured them into the tank. One fish, a small cardinal tetra, immediately panicked, bashing itself back and forth until it eventually fled and hid under a rock. The little girl, laughing with excitement, exclaimed
- Why is it so afraid?!
- Maybe it’s afraid of being eaten by the bigger fish, I answered.

The girl looked at it empathetically. Then another fish, a small goldfish, was poured into the tank. This fish didn’t seem the least worried about its new home, hardly inspecting the surroundings before immediately setting off to feed on the falling food flakes.
- This fish is not afraid, my niece said. Doesn’t the bigger fish like to eat him to?
- Yes, but maybe he doesn’t know that the bigger fish wants to eat him, I said.
- Why? she asked.
- Well, the goldfish come from a different background than the tetra, with no big fish around to hunt him. Neither was his parents ever chased by any big fish.

The girl looked at me deeply impressed.
- How come you know so much about these things? She asked.
- It’s kind of my job, I answered proudly.
- Really? she said. I thought your job was to write boring things on the computer all day!
- Well, that also, I replied…

The tetra and the goldfish do indeed come from very different backgrounds. The cardinal tetra was likely caught in a wild jungle stream somewhere in South America, whereas the goldfish stemmed from an industrial breeding facility where its line had been bred for generations. The two fish clearly responded differently to my aquarium, one seemingly acutely risk-aware, the other almost naïvely ignorant of any potential threat (The goldfish eventually got eaten, but so did the tetra…). This thesis is about animal behaviour; why and how it may differ between animals from different backgrounds. It’s about taking risks and being bold in the face of danger, but also about the need for safety and the importance of social company.

1 Introduction

1.1 Behavioural trade-offs

Why animals behave in certain ways under certain conditions is the magna quaestio in behavioural ecology. Behaviours are highly flexible traits, allowing animals to quickly adjust their phenotype to changes in environmental and social conditions. Trait flexibility provides the basis for a choice driven response in animals, where actions are the results of decision-making processes aimed to optimize short and long term fitness of the acting individual (Krebs & Davis 2006; Stephens 2008). Incorporated in such decision process is often a balancing between conflicting demands of the animal, presumably with the animal behaving according to a cost benefit assessment of likely outcomes (Krebs & Davis 2006). Trade-offs between conflicting behaviours is thought to be a fundamental part in how animals interact with its environment and social surrounding (Dill 1987). How animals trade between such conflicting behaviours, and the factors underlying the trade-off decision, is a central theme in this thesis.

In many cases, animal decision making appears to reflect an adaptive trade-off between the need to avoid predation and various other needs (Lima & Dill 1990). The balance between predator avoidance and foraging are considered particularly important, as both actions may have strong impact on individual fitness (Dill 1987; Stephens 2008). Foraging provides energy and growth to the animal, but often reduces vigilance and thus increases predation risk. The trade-off therefore commonly involves a compromise in the time an individual diverts to foraging under risk vs. the time spent not foraging in safety (Magnhagen & Magurran 2008). How time is allocated should ultimately depend not only on the immediate risk confronting the prey, but also on the overall risk experienced by the prey during recent history, i.e. involving risk experienced at other times (Lima & Bedenkoff 1999). For example, intuitively one may predict animals to reduce foraging under risk of predation, but under a constant predation threat prey might be forced to forage actively even in the presence of predators (Ferrari et al 2009). Such dynamics may explain why predator sympatric individuals have been reported to be both more risk prone (e.g. Riesch et al 2009; Brown et al 2007), and less risk prone (e.g. Kelly and Magurran 2003a) than predator naïve individuals. This thesis investigates how animals with different predation background allocate time in response to predation risk.

An animal may also reduce its risk of predation by joining others, often conspecifics, in groups. Grouping act as an anti-predator behaviour through mechanisms such as risk dilution, increased vigilance, and predator confusion, but may also entail costs for the individual in terms of increased resource competition (Krause & Ruxton 2002). Hence, it may benefit an individual to be social under risk of predation, but less so when exploiting a food resource. The size of the group may balance potential costs and benefits of group living (Krause & Ruxton 2002). As groups gets larger, individual predation risk may decrease through e.g. risk-dilution, but predation risk may also increase as larger groups more readily attract predators. Likewise, a large group may intensify foraging competition among the members, but may also provide foraging benefits in terms of enhanced cooperation in attacking and finding food. The animal may hence not only decide whether or not to join a group, but may also have to trade between joining groups of different sizes. Such decision is likely to be based on the current ecological conditions experienced by the animal, such as food availability and predation environment (Hoare et al 2003).

Group size may also affect behaviour of the group members. If individual predation risk is negatively correlated with the size of the group, individuals may be more willing to take risks in larger groups. Likewise, if competition increases with group size, individuals may be forced to compensate this by being more risk-prone in their foraging (Grand & Dill 1998; Bohlin & Johnsson 2004). Social processes within a group may uniform behaviour among group members, as individuals tend to mimic the behaviour of the group majority or dominant members (Ward et al 2008; Harcourt et al 2009). For group-living fish, conformity may be adaptive, both as a way to reinforce the anti-predator effect of the group and to avoid being selected out and attacked by a predator (Pitcher and Parrish 1993). The trade-off between maintaining conformity and optimizing individual preference may depend on the size of the group. Webster & Ward (2011) suggest that behavioural conformity may increase with group size, although emphasize this relationship to be largely unexplored. This thesis investigates how grouping affects behaviour, and how animals choose between different group sizes depending on context.

Fish are able to make accurate assessments of their risk of predation, and to trade risk in an adaptive way (Milinski 1986; Kelly 2008). Fish anti-predator behaviour, such as schooling and predator inspection, and various risk-taking trade-offs, such as choosing between shelter and foraging in the presence of a predator, is known to be fine-tuned to local predation conditions and hence differ between fish populations living under contrasting predation regimes (Magurran et al 1993; Magnhagen 2006). Behaviour related to predation response has traditionally been thought to have a strong genetic base, allowing even young individuals to respond correctly to predators (Kelley and Magurran 2003b). Heritable differences in risk-taking and anti-predator traits between populations have also commonly been found (Huntingford & Wright 1993). One have argued that experience within an individuals life-time should have low influence on predation related behaviour, as failing to react correctly to a predator may mean death to the prey and hence no second chance to learn from experience and change the behaviour (Kelley and Magurran 2003b; Magnhagen and Magurran 2008). Today however, more and more studies report experience to have a profound effect in shaping risk-taking and anti-predator behaviour, and to contribute to phenotypic diversity both within and between population (Stamps 2003; Chapman et al 2008; Chapman et al 2010). The way experience shape behaviour, and how prey rely on experience over time is still not fully understood, although several studies point to potential complex dynamics. For example, experience early in life may have long lasting effects on risk-taking behaviour, and may potentially constrain behavioural adjustment later in life (Chapman et al 2010). Experience of high–risk predators may have longer longer lasting behavioural effects than experience of low-risk predators (Ferrari et al 2010b). Further, depending on environmental stability and predictability, the time-span an animal is affected by past experience, may have adaptive significance, e.g., a short memory may be advantageous in fluctuating conditions (Ferrari 2010a). Understanding the plasticity of risk-taking behaviour, and the extent to which geographic variation in risk-taking and anti-predator behaviour is shaped by predation induced selection or by fish adjusting behaviour by learning through experience, is important knowledge when investigating behavioural trade-offs and the mechanisms underlying local adaptations of populations (Foster and Endler 1999; Mousseau et al 2000). This thesis investigates the influence of genes and experience on risk-taking phenotype, as well as the flexibility of risk-taking behaviour in prey.

1.2 Consistent individual variation

Over the last decades, the study of behavioural variation and trade-offs have shifted focus from primarily considering behavioural variation as relevant solely between species, to a recognition that variation is present also within species, and even within populations (Foster and Endler 1999). Today, variation at the level of the individual is being intensively studied (i.e. animal personality), and accumulating research indicates extensive presence of consistent differences in behaviour between individuals stemming from similar ecological conditions (Gosling 2001; Réale et al 2007). A few distinct behavioural dimensions (or traits) are used to define animal personalities in an ecological context (Réale et al 2007). Consistent individual variation in risk-taking (following repeated measures in the same environment) is often referred to as boldness, and is commonly associated with how predation-risk is traded (Toms et al 2010; Conrad et al 2011). Similarly, temporal and contextual consistency in the degree of social attraction to conspecifics has been singled out as a personality dimension, commonly referred to as sociability (Réale 2007). Integrated in the concept of animal personality are trait correlations, or behavioural syndromes, whereby two or more personality traits co-vary across time and context (Sih 2004). An active field of research is investigating how general the presence of behavioural syndromes is in the animal kingdom, and their role in constraining behavioural trade-offs.

An individual behaviour that is consistent and non-flexible over time and contexts, does not fit easily into the traditional framework of evolution and ecology (Dingemanse & Réale 2005, Wolf et al. 2007). According to fundamentals of natural selection, a trait phenotype should be clustered around an optimized mean, from which deviations are to be considered noise, eventually to be selected against and disappear in a stable environment (Krebs & Davies 2006). Thus, the notion that individual variation in trait characteristics actually could be an ever present element in a species or a population may seem puzzling from an adaptationist point of view (Bell 2007; Wolf et al. 2007). Several mechanisms and processes have been proposed to explain behavioural inflexibility and the presence of consistent individual variation. Physiological and cognitive constraints inherent in the animal may make behavioural adjustment both time and energy consuming (Dewitt et al. 1998). If information on the immediate future is unreliable, investing in behavioural change may hence be risky and the animal may be better off sticking to a fixed phenotype (Dewitt et al. 1998). Frequency dependent selection may maintain individual variation, as may variation in fitness due to fluctuating environments (Bell 2007; Dingermanse 2004). Investigating the presence of consistent variation in risk-taking and social behaviour at both individual and population level is an important aim in this thesis.

2 Objectives

This thesis aims to extend the knowledge of how animals compromise behaviour depending on environmental background and context. The focus is on between- and within-population variation in risk-taking and social trade-offs in Eurasian perch. Specific issues addressed are the following:

1. Influence of inheritance and experience on risk-taking phenotype (Paper I & II)
2. Effect of predation background on risk-taking phenotype (Paper I & II)
3. Influence of past and current experience on risk-taking phenotype (Paper I & III)
4. The relationship between group size, risk-taking and social behaviour (across contexts) (Paper IV & V)
5. Presence of consistent individual variation and behavioural correlations in risk-taking and social behaviour. (Paper I, IV & V).

3 Materials and Methods

3.1 Study Species

Eurasian perch (*Perca fluviatilis)* is used as study species in this thesis. Eurasian perch is a widely distributed fish in fresh and brackish water systems throughout Europe, and Northern Asia (Collette & Banarescu 1977). It is an ontogenetic omnivore with strong cannibalistic tendencies, and population structure and dynamics are often clearly characterized by the predation environment (Persson et al. 2000). Spawning occurs in spring in shallow water around vegetation and sunken dead wood. The larvae hatch the same spring and immediately migrate out to the pelagic zone where it feeds on zooplankton. During late summer, the young fish again move into the littoral zone and gradually shift diet towards macroinvertebrates as they increase in size (30-80 mm) (Byström et al 2003). As perch gets even bigger, the proportion of fish in the diet increases. Both adults and juveniles are easy to catch and rear, as well as maintain under experimental conditions.

3.2 Study lakes and populations

Perch from two populations were used in the behavioural experiments conducted throughout this thesis. The populations originated from lake Ängersjön and lake Fiskjön, both lakes located within close range to Umeå, Sweden (63°47′ N; 20°17′ E).The lakes are similar in size, depth, productivity and amount of littoral vegetation (Magnhagen & Heibo 2001; 2004 - Table 1). They share similar fish communities, dominated by perch, pike (*Esox lucius*) and roach (*Rutilus rutilus*). Ruffe (*Gymnocephalus cernuus*) is also present, as is bream (*Abramis abramis*), ide (*Leuciscus idus*) and burbot (*Lota lota*), although in lower numbers.

The two lakes differ in the size structure of the perch population, with Fisksjön in general having a high density of similarly sized, small perch (stunted), while the size of the perch in Ängersjön is more evenly distributed and on average larger (Magnhagen & Heibo 2001; 2004; Magnhagen 2006). The magnitude of difference between the lakes, both regarding size structure and perch abundance, varies considerably between years (Paper II in this Thesis).

Most males (90-99%) are mature at the age of 2 years, and most females between 3 and 4 years of age in both lakes (Heibo & Magnhagen 2005). Females are larger at maturity in Ängersjön compared to Fisksjön (17.2 cm vs. 11.5 cm) (Heibo & Magnhagen 2005). Cannibalistic predation pressure on young of the year (YOY) perch have been estimated based on abundance and size-structure of the perch population, and predation is in general higher in Fisksjön compare to Ängersjön (Magnhagen 2006; Paper II in this Thesis).

Table 1. Physical characteristics of the two lakes used in the thesis (from Department of Environment, City of Umeå).

Lake	Location	Area (km2)	Mean Depth (m)	Max Depth (m)	Total P µg^{-1}	Total N ug l^{-1}
Ängersjön	63° 37´ N; 19° 48´ E	1.45	0.9	3.5	21	230
Fisksjön	63° 42 N; 20° 08´ E	0.75	1.9	3.1	18	290

3.3 Data collection and rearing of fish

Young of the year (YOY) and one year old (1+) perch were used as experimental subjects throughout this thesis. The perch had either been caught in the wild, or been reared in a controlled environment. The reared fish were collected as eyed eggs in the littoral zone of the lakes after the perch had spawned (early May), and stocked in a semi-natural pond at a university facility close to Umeå were they subsequently hatched. The pond was divided in two equally sized sections by an impenetrable plastic barrier, having perch from Ängersjön in one section and perch from Fisksjön in the other. The pond contained no other fish than the stocked perch, but had natural resources of zooplankton and macroinvertebrates for the fry to feed on. In September, the pond-reared perch were collected by beach-seining, and transported in aerated tanks to the Umeå Marine Research Station (UMF), 45 km south of Umeå. At UMF, fish were kept by lake origin in large indoor storage tanks with continuously running water. Water temperature and light regime were set to follow the natural conditions for the time of the year. While in storage tanks, all fish were fed with frozen chironomids ad libitum, the amount of chironomid larvae varying depending on the water temperature and stocking density. The tanks had artificial vegetation to use as shelter for the fish.

Concurrently with the beach-seining of the pond reared fish, wild young of the year perch were collected by beach-seining in the littoral zone of the lakes, and transported in aerated tanks to UMF were they were kept under identical conditions as the reared fish.

3.4 Behavioural experiments

Central to this thesis are observational studies on perch in aquaria. All fish used in the behavioural experiments had been individually marked using alcian blue or tattoo paint on their caudal fin to allow for identification within a group of maximum eight fish. Marking was done on anaesthetized (MS222, 250 mg/l) fish. Behavioural experiments started with moving fish from the storage tanks to the experimental aquaria where they were allowed time to acclimatize. The experimental aquaria (95×41×44 cm – 170 l) were housed in two identical rooms in close vicinity of the storage tanks. Each room had 8 aquaria, each supplied with continuously running water (14-18ºC). Light regime was similar to natural conditions.

3.4.1 Boldness test

Important to all five papers in the thesis is the quantification of risk-taking behaviour in perch (boldness). This was done using a version of the so called open field test, in which the perch, usually in groups of four, were observed foraging in front of a large predator. The aquaria were divided in three equally sized sections (Figure 1). One section contained the predator (a large perch, 15–22 cm long), while the two other sections contained the group of young perch. The section containing the predator was separated from the rest of the aquarium by a plastic net (mesh size 5mm), making it possible for the perch to see the predator but not for the predator to physically attack them. The section farthest away from the predator was covered with artificial vegetation (green plastic ribbons), while the section closest to the predator was open with no vegetation. Artificial vegetation was also present in the predator section. The small perch could move freely between the vegetated and the open areas. The bottom of the aquarium consisted of gravel.

An opaque screen was used to cover the plastic net during acclimatization of the small perch and between observations, to prevent the perch from seeing the predator. To minimize predator olfactory cues between observations, the water flowed into the section containing the young perch and out through the predator section.

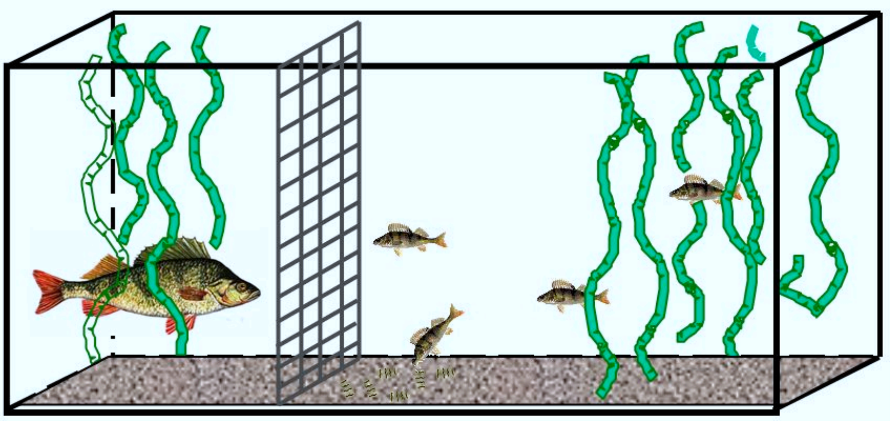

Figure 1. The aquarium set-up used to measure boldness in young of the year perch. The young perch could choose to stay in the vegetated area, far from the predator or enter the open area to feed. A plastic net separates the predator from the prey.

The boldness test started with moving the opaque screen from the plastic net towards the vegetated section, by this enclosing the group of perch in the vegetated section. Chironomid larvae, corresponding to 3% of the total fish weight, were then poured into the open section, just in front of the plastic net close to the predator section. The larvae were evenly distributed alongside the net and allowed to sink to the bottom. Thereafter, the opaque screen was removed, making the large perch visible to the smaller perch, and the observations started. The perch now had the choice of eating in the open area, exposing themselves to the predator, or staying behind in the vegetated area, further away from the predator.

Observation sessions usually lasted for 10 minutes, during which the behaviour of each individual fish was recorded by an observer sitting in front of the aquarium.

Up to four different activities were recorded depending on objective; occurrence in the vegetation, occurrence in the open, latency to feeding and predator inspection. The behavioural measurements reflects slightly different aspects of boldness, such as taking decisions on when to increase risk by leaving the shelter, to decrease vigilance when feeding, and whether to remain in the risky area or return to shelter. The observer entered all behavioural data directly into a computer, using a program that recorded every second of the observation period. A visual overview of how the behavioural records could be structured can be seen in figure 2. After each observation period, the opaque screen was put back next to the net. Experiments usually included two or three observation periods (runs) per group of perch. Commonly, eight to twelve replicates per experimental unit (e.g. 12 groups per lake) were used in a study. After each study, the fish were killed by an overdose of MS222. Predators were either released or kept in a storage tank for further use.

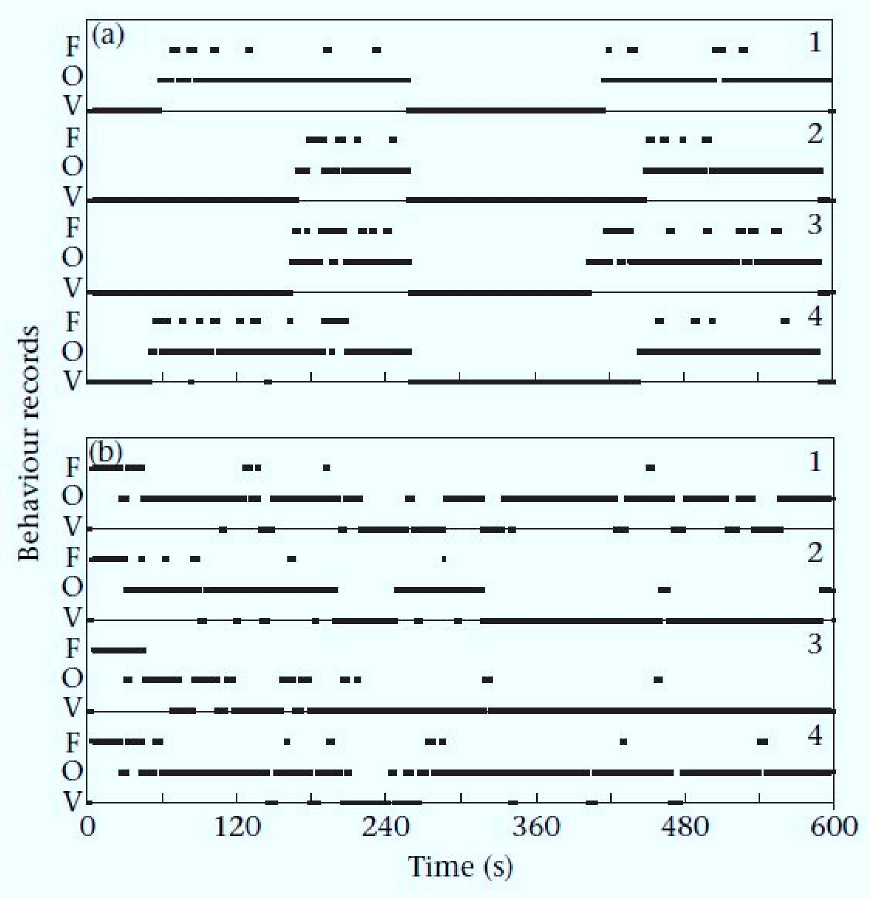

Figure 2. Example of behaviour records from a 10-min observation of one group of four young of the year perch from Fisksjön (a) and one group from Ängersjön (b), V: perch in vegetation, O: perch in open water, F: perch feeding on chironomids (adapted from Magnhagen & Borcherding 2008).

3.5 Analytical approaches

Several analytical methods were used in this thesis. Principal components analysis (PCA) is a multivariate technique useful when you have observations on a number of variables and wish to develop a smaller number of artificial variables (components) that will account for most of the variance in the observed variables (Zuur et al 2007). In paper I, II, IV and V, PCA is used to reduce the number of behavioural measurements taken in the boldness test, into more general boldness scores. In all papers, the first component (PC1) explained over 50% of the variation in the data, and consisted of variable loadings that unambiguously reflected a risk-taking gradient. PC1 was hence used as a general boldness score and treated as a response variable in further analysis.

All behavioural experiments involved repeated measures on several unit levels (e.g. aquaria, group, individual etc.). To avoid pseudoreplication (i.e. that multiple measurements on the same unit are treated as independent data points, thereby inflating the sample size) mixed effect models were used throughout this thesis. Mixed effect models allow for incorporation of both fixed and random effects into the model. Fixed effects are the explanatory variables for which we want to test the differences of the response variable between factor levels (e.g. difference in mean boldness between Fisksjön and Ängersjön perch). Random effects are variables that may influence the variation of the response variable, but for which we do not have a particular hypothesis to test (e.g. difference in boldness between aquaria, difference between individuals within group etc.). The behavioural experiments often involved repeated measurements of several correlated random effects, and this was tackled by incorporating nested random effect structures into the models, thereby managing correlated observations within a hierarchy of experimental units. Also, variance component analysis of the random effects was used to get an estimate of how much of the variation in the response variable could be attributed to a given random effect. When response data was normal, general linear mixed effect models were used (LMM), otherwise generalized linear mixed effect models (GLMM) were applied (e.g. for binomial response data). In paper III, generalized additive mixed models (GAMM) were used to analyse non-linear relationship between a binary response variable and a continuous explanatory variable.

Model selection is used in paper I, III, IV, and V, as a tool to evaluate effect of explanatory variables. Model selection techniques aim to find the best (most parsimonious) model out of a candidate set of models, by balancing the “goodness of fit” of models with the complexity of the models. Two selection methods are used; model ranking via Akaike Information criteria (AIC), and stepwise regression techniques via Likelihood ratio tests. AIC based selection does not provide a “null hypothesis test” of a model in the same way as stepwise regression does, but only rank models by balancing model accuracy and complexity, giving the most parsimonious model the lowest AIC.

3.6 Predation estimation

An important and recurring subject in all five papers is the effect of predation on perch behaviour. One of the most severe threats for young perch is that of being cannibalized by one of its larger conspecifics (Treasurer 1989; Persson et al 2000). Based on the size of a cannibal perch, one can estimate the number of attacks it will perform daily at different prey sizes, using individual based models (developed by Persson et al. 2004). The models incorporate the size range of prey accessible to a specific size of the cannibal perch, as well as the predator voracity (Lundwall et al 1999; Persson et al 2004). Given the size distribution and relative abundances of the perch populations in lake Fisksjön and Ängersjön (information that was collected by fishing surveys using Nordic standard survey nets), and given the size-specific relative attack rates for cannibalistic perch produced by the predation model, one can calculate lake-specific predation pressure for different sizes of prey. Paper II uses this method to compare predation pressure on different sizes of YOY perch between Fisksjön and Ängersjön over several years, and the method is also referred to in paper I, III and V.

3.7 Description of the experiments

3.7.1 Paper I

The paper used a common garden approach to investigate patterns in the influence of inheritance and experience on differences in risk-taking between YOY perch in lake Fisksjön and lake Ängersjön. Eggs were collected in May from both lakes and were hatched and reared in a pond under identical conditions, free from predation. In September, both the pond reared YOY and wild YOY from both lakes were collected for boldness tests. Differences in boldness between the four ecotypes (Fisksjön Pond; Ängersjön Pond; Fisksjön Wild; Ängersjön Wild) were tested using LMM based on boldness score derived via PCA.

3.7.2 Paper II

Six years of data from boldness tests of wild YOY perch from Fisksjön and Ängersjön were correlated with corresponding estimations of lake-specific predation pressure on YOY, generated from yearly fishing survey data. General linear mixed models were used to test for effect of lake and year on boldness, and variance components were calculated to investigate the influence of various random effects, such as between lakes and between years, on total explained variance.

3.7.3 Paper III

Short and long term effects of predator experience on risk-taking behaviour were investigated by comparing wild and pond reared perch from Fisksjön. Approximately 4 months after hatching, wild and pond fish were captured and transferred to UMF where they were kept in storage tanks. Fish were tested for boldness at two occasions; a few days after capture, and nine months after capture. Different fish were used at the two test occasions. Differences in boldness between wild and pond fish at each test occasion was tested using generalized linear mixed models (GLMM). Short term behavioural adjustments both within and between repeated test-runs were investigated using generalized additive models

3.7.4 Paper IV

Paper IV investigated the effect of group size on boldness and social conformity using 1 year old perch originating from Ängersjön. The perch had been collected as eggs and reared 5 months in the pond, and then beach-seined and transferred to UMF were they were kept in the storage tank for 13 months before being tested for boldness. Boldness tests were performed on perch in five different group sizes; one, two, three, five and eight fish respectively. Social conformity in a group was assessed based on dyadic relationships between group members. Dyads were considered associated (behaving uniformly) if both individuals resided in either the open section or the vegetated section of the aquaria at the same time. To compare conformity among group sizes, the total dyadic associations in a group was divided by the number of possible dyadic combinations specific to the size of the group. Differences between group sizes in behavioural conformity and boldness were analysed using logistic regression and LMM.

3.7.5 Paper V

Effects of context and personality on group-size preference were tested by behavioural studies in aquaria using wild caught YOY perch from lake

Fisksjön and Ängersjön. The aquaria were divided into three equally sized areas using two plastic nets (Figure 3). The two outer areas contained either a group of two or a group of eight young perch. The focal individual was placed in the middle section of the aquaria. Context dependent group-size preferences was tested by making fish choose association with either the large or the small group in three different contexts; when the small group was feeding (chironomid larvae), when the small group resided in shelter (simulated by green, plastic ribbons), or a control treatment with no other stimuli than the small and the large group, respectively (Figure 3). The effect of context on group-size preference was tested using logistic (multinomial) regression. Individual behavioural consistency across contexts and time was investigated by correlating individual behaviour both between contexts and between observation sessions. Perch used in the group-size preference test were also subjected to boldness tests, to investigate correlation between individual group-size preference and boldness.

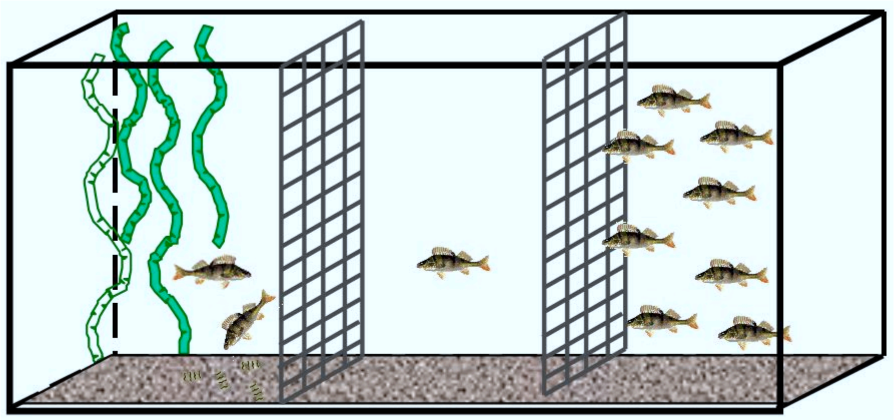

Figure 3. Experimental set-up of the group-size preference test (performed with either only fish, vegetation on the small shoal´s side, or food on the small shoal´s side.

4 Results

4.1 Paper I

The wild fish differed in risk taking, with fish from the lake Ängersjön (low predation-risk population) acting bolder than fish from lake Fisksjön (high predation-risk population) (Figure 4). Both populations of the pond reared fish were equally bold. Only the fish originating from lake Fisksjön showed different behaviour when comparing wild and reared ecotypes.

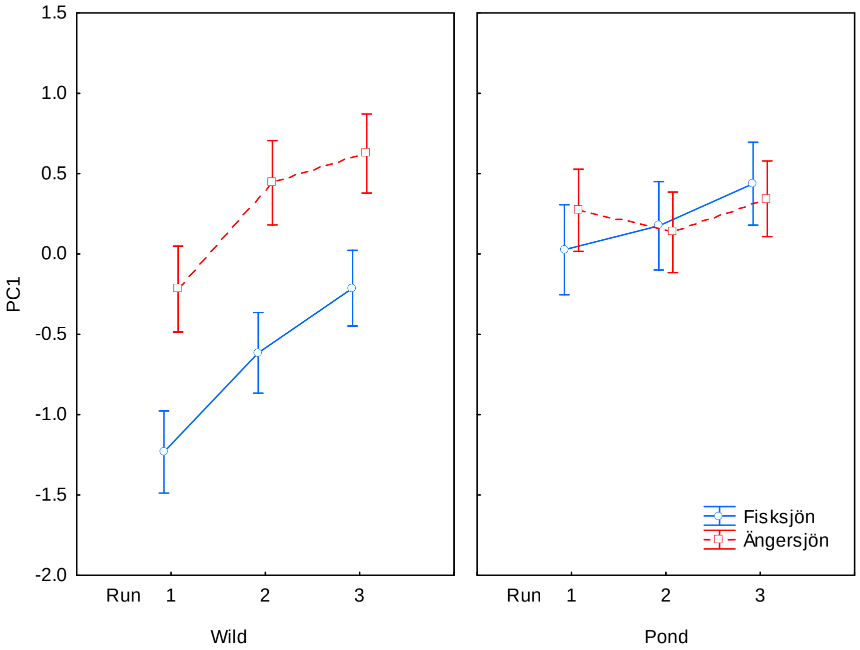

Figure 4. Risk-taking score for four ecotypes (Fisksjön Wild, Ängersjön Wild, Fisksjön Pond, Ängersjön Pond) based on PC1 (mean ± 95% CI) estimated by Principal Component Analysis on 184 fish. High scores indicate long time in the open, short latency to start feeding and short latency to enter open. Number of replicates was 12 for each ecotype, except for Fisksjön Pond, where N = 10.

4.2 Paper II

YOY boldness was significantly correlated with the year-specific estimates of cannibalistic attack rates, with lower boldness scores in years with higher predation pressure. Both lake and year had an effect on YOY boldness, and Fisksjön perch were consistently shyer compared with those in Ängersjön, although the magnitude of the difference varied among years. Yearly fluctuations in population structure, predation risk and boldness scores were larger in Fisksjön than in Ängersjön (Figure 5). Variance component analyses showed that differences between lakes in boldness scores only explained 12 per cent of the total variation, similar to the differences between years.

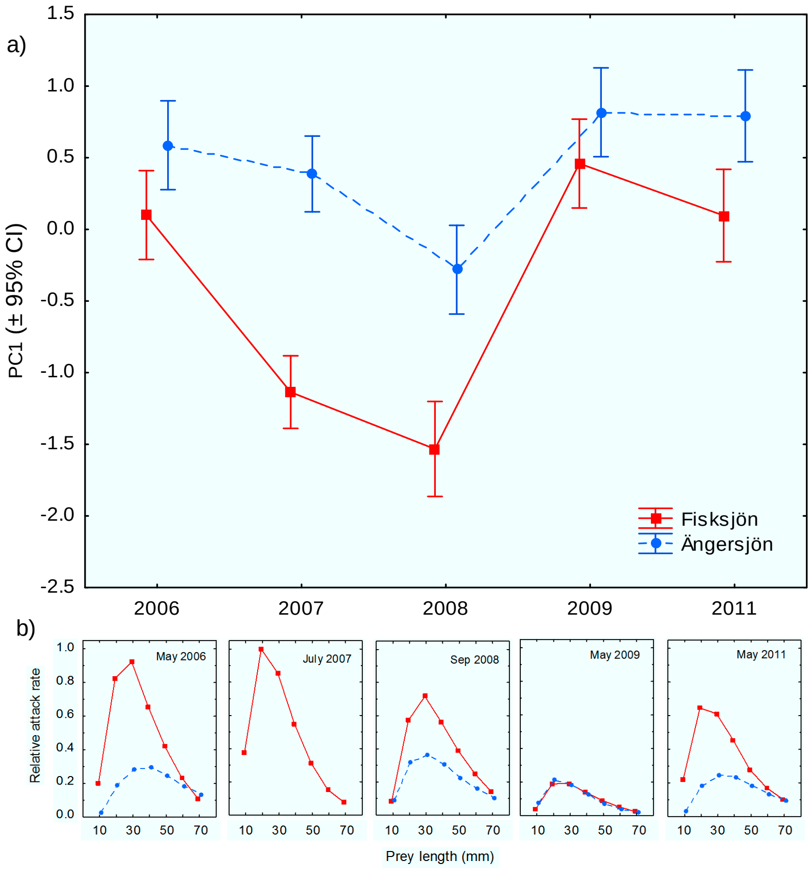

Figure 5. a) Average boldness score (PC1 ± 95% CI) for young-of-the-year perch in Fisksjön (solid line) and Ängersjön (broken line) tested in aquarium studies during 5 years (2006 – 2011). b) Relative cannibalistic attack rates on different lengths (mm) of perch estimated from an individual-based model (Persson et al. 2004), using cannibal size distribution and abundance in fishing surveys carried out 2006-2011 in Fisksjön (solid line) and Ängersjön (broken line, not sampled 2007). Attack rates are presented as proportions of the highest estimate.

4.3 Paper III

Wild and pond reared fish differed in boldness, with the predator experienced fish (Wild) being significantly less bold compare to the predator naïve fish (pond) at both test occasions; i.e. immediately after capture and after nine months in a predator free environment. Behavioral adjustment predominantly occurred between runs, and not within runs (Figure 6).

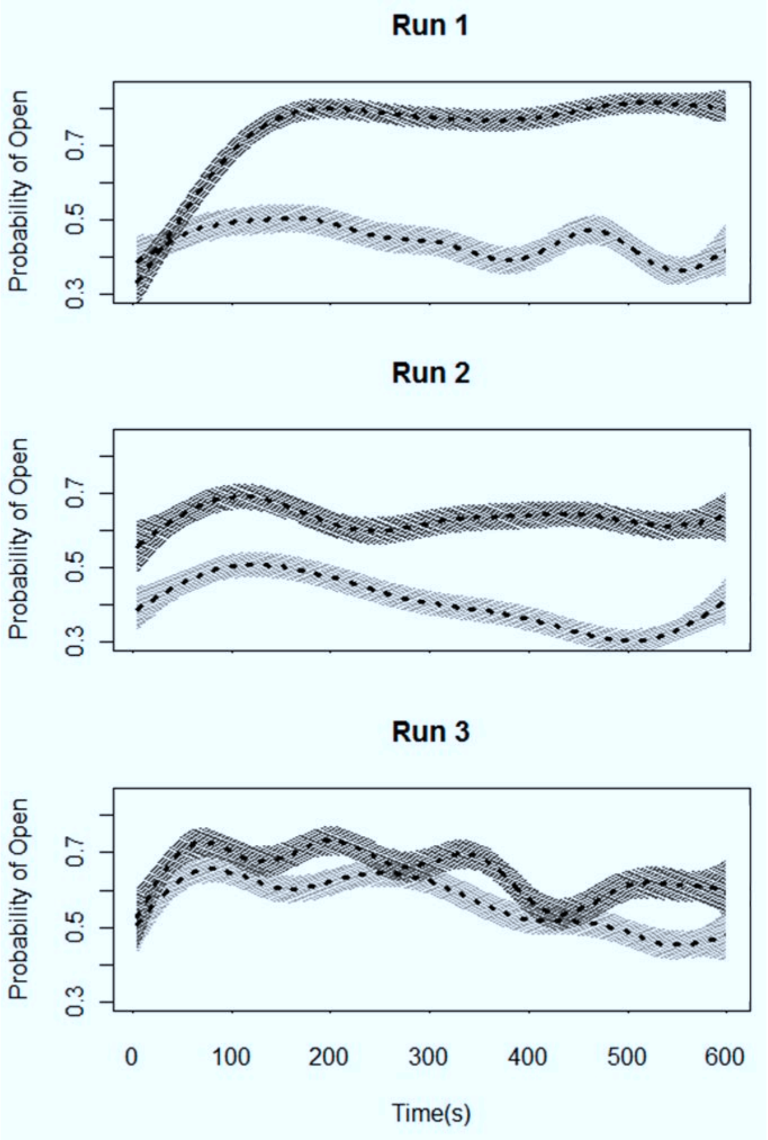

Figure 6. Probability profiles of boldness over time for 4 months old Wild and Pond fish across three runs. The dotted lines are the fitted values from a generalized additive mixed effect model with binomial errors, and represent averages of several groups per ecotype. Lines are embedded with 95% confidence shades (dark = Pond; light = Wild).

4.4 Paper IV

Risk-taking behaviour was significantly affected by the size of the group, with solitary perch being significantly less willing to take risks than perch from groups consisting of two, five and eight fish. Behavioural conformity tended to differ among group sizes, with a trend towards less conformity in bigger groups.

4.5 Paper V

In general, the perch associated more with the large group than the small group, but significantly less so during the food treatment (Figure 7). The vegetation treatment did not affect group-size preference compare to the control treatment. Consistent individual differences in group-size preference were found within each context and also between the control and the vegetation treatment, but could not be established between the food and the control treatment, or between the food and the vegetation treatment. Further, no correlation was found between an individual's boldness and its group-size preference in any of the three contexts, or for any of the two lakes.

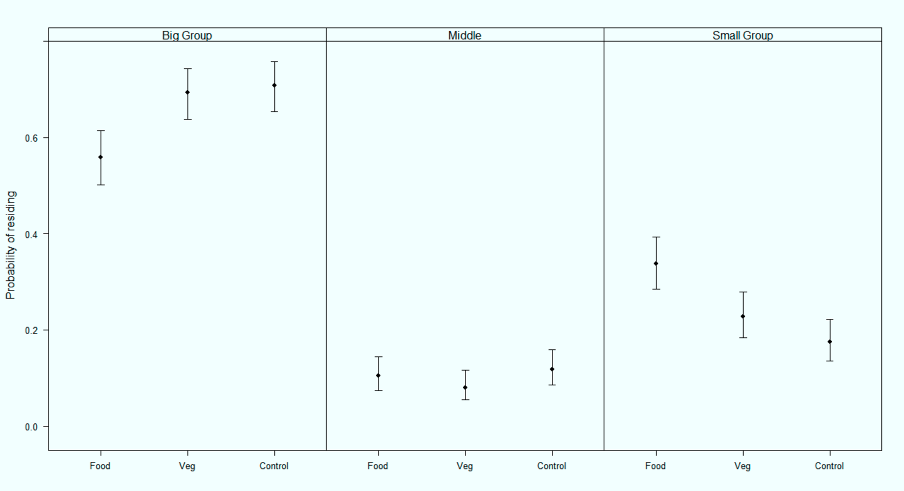

Figure 7. The probability (mean ± 95% confidence intervals) of fish residing near the big group, in the middle section or near the small group depending on treatment. Probabilities are derived from a logistic regression model (multinomial).

5 Discussion

Several findings in this thesis show predation as the main force shaping risk-taking behaviour in the studied perch populations. Lake-specific predation pressure corresponded to annual variation in risk-taking behaviour between the populations (Paper II), and fish originating from predator free environments differed in risk-taking from fish exposed to a high predation pressure (Paper I & III). The results reinforce conclusions made by Magnhagen (2006) and Magnhagen & Borcherding (2008) that differences in predation pressure underlie inter-population phenotypic differences in the studied system, and is in line with the view of predation as a fundamental agent shaping animal behaviour and risk-trading (Lima & Dill 1990). The perch responded to predation by becoming less bold, as is illustrated by the pond reared, predator naïve fish from Fisksjön being bolder than the wild fish (Paper I and III), and also by the lower boldness score in years with high predation pressure (Paper II). Such negative relationship between predation pressure and boldness supports the prediction that animals should make trade-offs towards safety when risk increases (Lima & Bednekoff 1999), and contradicts studies reporting boldness to increase with predation experience (e.g Brown et al 2007, Ferrari et al 2009).

Little is known about the mechanism by which predation generates risk-taking phenotypes in animals. Predation is considered a strong selective force and increased predation will quickly reshape the distribution of phenotypes in a population (Magurran 1999). Inter-population phenotypic variation in traits linked to predation responses has been reported to have a strong genetic background (Giles 1984; Breden et al 1987; Huntingford and Wright 1993; Riechert and Hall 2000). However, if predation pressure fluctuates, a genetically fixed risk-taking phenotype may be maladaptive as it can not be fine-tuned to current conditions. Paper II revealed strong inter-annual variation in predation conditions in the studied populations, especially for perch in lake

Fisksjön, hence seemingly benefitting individuals that are able to estimate current predation pressure and adjust its behaviour accordingly (Ferrari et al. 2010a). Such reasoning fits with the strong influence of experience on risk-taking concluded in paper I, II and III. The fact that the difference in risk taking between the wild populations from Fisksjön and Ängersjön in Paper I and III, did not persist when the populations were reared in a common environment, suggests the variation observed between the two wild populations is caused by individuals adjusting its behaviour to environmental conditions, and not due to genetically fixed phenotypes. Also, the correlation between risk-taking behaviour and year-specific estimates of predation pressure seen in paper II, indicates inter-population variation to be shaped by direct phenotypic responses to recent experience of predation risk, rather than a consequence of inherent traits shaped by divergent selection. The results fits into a growing number of studies reporting experience to underlie most or some of the phenotypic variation in risk-taking traits seen between populations (Kelley and Magurran 2003a,b; Brown et al 2007; Riesch et al 2009).

Few studies have investigated how animals rely upon predation experience over time. This thesis concludes long lasting behavioural effects in perch following exposure to predation. Differences in risk-taking between predator experienced and predator naïve perch from Fisksjön were still present nine months after the last exposure to predation, with the predator experienced fish continuing to display the most risk-averse behaviour when confronted with a predator (Paper III). An adaptive retention time of a learned anti-predator behaviour should reflect the current predation conditions (Ferrari et al 2010b). Continuing to be risk-averse under conditions that have been predator free for a long time may be maladaptive, e.g. by the individual becoming less competitive in a foraging context. Still, even if the likelihood of predation is low, failing to remember an anti-predator response if predation conditions were to change, may be lethal. Such trade-offs between the past and the present may play part in how experience of predation shape behavioural phenotype in prey.

Despite the long lasting effects of prior predator experience seen in paper III, perch were quickly able to adjust behaviour following learning of current conditions. Adjustment of risk-taking behaviour during observation sessions, often with the animal becoming bolder over the course of the repeated trials, occurred in all five papers. Hence, although the influence of past predation experience was maintained in stable environments, it seemed relatively easy to shrug off following only three short repeated exposures to new conditions. This reinforces the notion of flexibility in perch risk-taking behaviour. Interestingly, such short-term behavioural adjustment predominantly could only be observed between trials, and not within trials (Paper III).

As may be predicted in a highly social fish like young perch, risk-taking was affected by group size, with solitary fish being less bold and did less foraging than fish in groups (Paper IV). However, perceived access to food reduced sociability (Paper V), demonstrating context dependency in perch group size preferences. Indication that grouping conform the behaviour of group members was found in paper IV, with the fish behaving more uniformly in larger groups.

Although the phenotypic variation between perch from lake Fisksjön and Ängersjön was found not to be stable over time (Paper II), extensive short-term behavioural stability was present at individual level. Consistent individual variation in both risk-taking and sociability was found in all five papers, confirming the existence of a "personality dimension" in perch behaviour. Although perch displayed large behavioural flexibility in response to current experience, a consistent personality type across context and time may potentially constrain such flexibility (Bell 2007).

This thesis concludes predation as the main force shaping risk-taking phenotype in perch. Experience had considerable influence in how predator avoidance was traded-off against foraging, with predator experienced fish being less bold than predator naïve fish. Little evidence was found to support a strong genetic contribution to phenotypic variation. Prior experience of predation had long lasting effects on boldness, but phenotype could quickly be adjusted in response to current conditions, indicating temporal flexibility in how experience shapes risk-taking behaviour. Strong social tendencies in young perch could be demonstrated, and social context affected how perch made risk-taking trade-offs. Behavioural plasticity, even in strongly fitness related behaviours such as risk-taking under the threat of predation, was evident, although potential behavioural constrains in the form of consistent individuality and long-term impact of experience, was also present.

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