Thesis for the degree of Doctor of Philosophy

INDIVIDUAL VARIATION IN BEHAVIOUR

personality and performance of brown trout in the wild

Bart Adriaenssens

UNIVERSITY OF GOTHENBURG

Department of Zoology, Animal Ecology
Box 463, SE 405 30 Gothenburg
SWEDEN

The oral defence of this thesis will take place at 10:00 am on Friday the 28th of May 2010, at the Department of Zoology, Medicinaregatan 18A, Gothenburg, Sweden. The opponent is Assistant Professor Alison M. Bell from the University of Illinois, Department of Animal Biology, School of Integrative Biology, Urbana, IL 61801, USA

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Bart Adriaenssens

Department of Zoology, Animal Ecology
University of Gothenburg
Box 463
SE-405 30 Gothenburg
SWEDEN
Email: bart.adriaenssens@zool.gu.se

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Front cover picture

Hieroglyph excerpt (row 58) from papyrus Berlin 3024 (1800 BC) entitled
‘Dispute between a man and his Ba’.

In ancient Egyptian belief, Ba symbolizes everything that makes an individual unique.
Transcript adopted by the author from Erman (1896).

To my wife, Maria Rosaria

DISSERTATION ABSTRACT

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Bart Adriaenssens (2010)

Individuals from the same population often show very different behaviour. These differences, when consistent across time, are referred to as animal personality or behavioural syndromes. Explaining the occurrence of animal personality from an evolutionary perspective has however proven a difficult issue to tackle. This thesis studies aspects of individual behavioural variation and personality in brown trout (*Salmo trutta*). More specifically, I investigate (1) to what extent variation in behaviour is consistent within and across contexts, (2) environmental and genetic effects on behaviour, (3) how this affects performance in the wild, and (4) whether this understanding can be used to improve rearing methods of supplementary hatcheries.

I found brown trout to express a wide variation of behaviours and provide evidence that much of this behavioural variation is associated in bigger behavioural syndromes. As a result, separate behaviours of brown trout cannot be considered as isolated units, but combine into clusters that sometimes are associated with non-behavioural measures such as body size or growth rate. Variation was further influenced by both inherited and environmental effects. *First*, individuals from different maternal and paternal origin differed in size, aggressiveness and response to novel prey or novel food. These results suggest that maternal and/or genetic effects influence behaviour and growth in brown trout (**I**). *Second*, reduced rearing densities in a hatchery increased the response to novel prey, food search ability in a maze and predator response (**II**). And *third*, hatchery trout were more successful foragers than wild conspecifics, yet showed less repeatable explorative behaviour across time (**III**). Personality traits were generally poor predictors of growth and survival upon release, suggesting that several behavioural strategies can be successful in nature. Nevertheless, in paper **IV**, slow exploring individuals grew faster than more bold trout. Furthermore, parr reared at reduced densities were twice as likely to survive in the stream as trout reared at high densities.

In conclusion, my results contradict simple associations between risk taking behaviour and growth-mortality tradeoffs under natural conditions. This challenges the recent view that individual differences in growth strategies can explain variation in behaviour and suggests more heterogeneous links between personality and life-history in nature (**V**). In addition, I show that reduced rearing hatchery densities facilitate the development of adaptive behaviour in brown trout, a finding that may have implications for current rearing methods in supplementary hatcheries.

Keywords: behavioural syndromes, personality, life-history, boldness, hatchery, survival, growth, foraging, anti-predator behaviour, learning, brown trout

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LIST OF PAPERS

This thesis is a summary and discussion of the following papers, which are referred to by their roman numerals:

I Höjesjö J, Adriaenssens B, Bohlin T & Johnsson IJ. Behavioural syndromes in juvenile brown trout (*Salmo trutta*); life history, family variation and performance in the wild. *[manuscript]*

II Brockmark S, Adriaenssens B & Johnsson JI. Less is more: density influences the development of behavioural life skills in trout. *[Proceedings of the Royal Society of London Series B-Biological Sciences, in press]*

III Adriaenssens B & Johnnson JI. Learning and context-specific exploration behaviour in hatchery and wild brown trout. *[manuscript]*

IV Adriaenssens B & Johnsson JI. No favors for the reckless: do personality traits predict fitness of brown trout in the wild? *[under review]*

V Adriaenssens B & Johnsson JI 2009. Personality and life-history productivity: consistent or variable association? *[letter to Trends in Ecology and Evolution, 24: 179-180]*

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INTRODUCTION

Individuals of the same population often differ considerably in the way they respond to challenges in their environment. To illustrate this, the figure below shows the movement pattern of brown trout fry when exposed to a novel object (**Figure 1**). Some individuals instantaneously investigate the novel object, whereas others remain at a distance. In humans, individual variation in behaviour is commonly referred to as personality, and has fascinated people since ancient Egyptian times (Erman 1896) whereas the study of personality in other animals is a more recent but rapidly emerging field (e.g. Magurran 1993; Gosling 2001; Sih & Bell 2008). This thesis studies aspects of individual behavioural variation and personality in animals. More specifically, I investigate (1) to what extent variation in behaviour is consistent within and across contexts, (2) environmental and genetic effects on individual behaviour, (3) how this affects social status and performance in the wild, and (4) whether this understanding can be used to improve rearing methods of supplementary hatcheries.

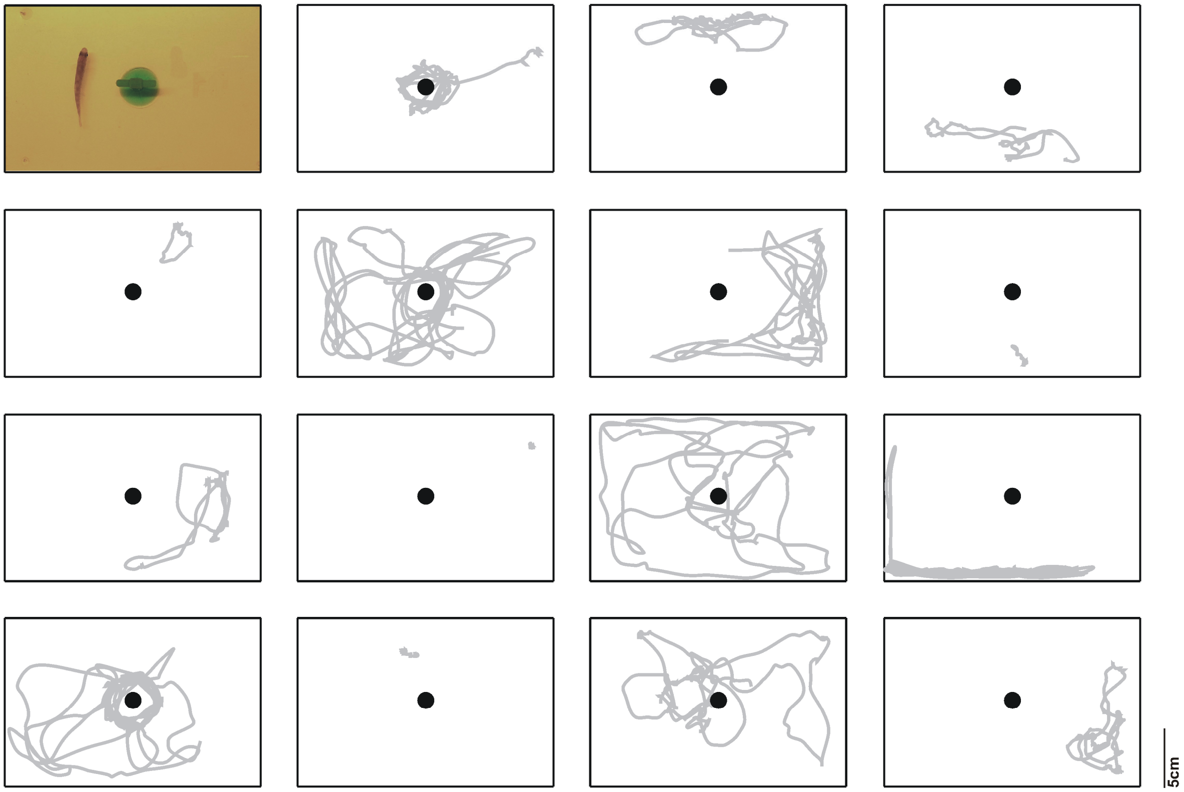


Figure 1 View from above on the movement pattern of 15 brown trout fry (*Salmo trutta*) during the two first minutes after exposure to a novel object (air tube plug). Swimming tracks were recorded with QuattroTrack software (Loligo Systems, Adriaenssens *unpubl. data*).

On behavioural variation, personality and behavioural syndromes

Historically, individual differences in behaviour have been considered as noise or random variation that should be accounted for in experimental design (Martin & Bateson 1990; Ruxton & Colegrave 2006). Indeed, some of this variation can, even under standardized laboratory conditions, arise from random differences in motivation between individuals (Colgan 1993). From an evolutionary point of view, however, individual differences in behaviour become more interesting when they are consistent across time. Individual consistency can occur in two distinct ways: across situations within the same behavioural context or across different behavioural contexts.

We speak of *animal personality* (Sih et al. 2004a; Dingemanse & Reale 2005) when the same functional behavioural category shows consistent variation between situations that differ in timing and settings. As a result, some individuals might generally be more aggressive than others. For example, three-spined sticklebacks (*Gasterosteus aculeatus*) that behave more aggressively against a conspecific intruder are generally also more aggressive against other species of territorial intruders (Huntingford 1976). In addition, other behaviours, for example activity level, exploration (response to a novel situation), boldness (response to a risky situation), and sociability (non-aggressive response to the presence of conspecifics) can be relatively consistent between situations in a wide range of animals (Bell et al. 2009). When animals demonstrate personality, individuals can be described according to their *behavioural type* (e.g. aggressive-inagressive, Sih et al. 2004a). In this thesis, I follow the view of Sih and Bell (2008) that personality not necessarily needs to have a genetic basis or needs to be stable over the *entire* lifetime of an organism. Animal personality is related to other phenomena described elsewhere in literature such as coping styles and animal temperament (differences are discussed in Réale et al. 2007).

Behavioural syndromes, result from covariance of individual behaviour across different contexts (Sih et al. 2004a; Sih et al. 2004b). For example, aggressive sticklebacks are also more bold in the vicinity of a predator (Huntingford 1976). Similar associations between bold behaviour and aggressiveness have now been demonstrated in a diverse range of model species (e.g. Riechert & Hedrick 1993; Bell & Sih 2007; Dochtermann & Jenkins 2007; Pintor et al. 2008).

Animal personality and behavioural syndromes imply that behaviour can be consistent across time, and can form integrated units together with other behaviours. This limited plasticity is surprising, because in nature it should to be optimal to adjust behaviour when it is appropriate in one context but not the other (Pigliucci 2001). Behavioural syndromes may therefore cause conflicts between behaviours, forcing individuals to make compromises rather than to achieve precision (Sih et al. 2004a). In North American fishing spiders (*Dolomedes triton*), for instance, individuals with superior prey hunting skills tend to be equally voracious against potential mates (*precopulatory sexual cannibalism*, Johnson & Sih 2005). Voracious spiders might therefore be skilled predators but can also end up having a lousy reproductive output (Johnson & Sih 2005). It is poorly understood how consistent behaviour pays off in nature and which selection processes maintain its variation between individuals (Magurran 1993; Wilson et al. 1993; Sih et al. 2004a; Dingemanse & Reale 2005; Réale et al. 2007).

Framework for the study of behavioural (co)variation

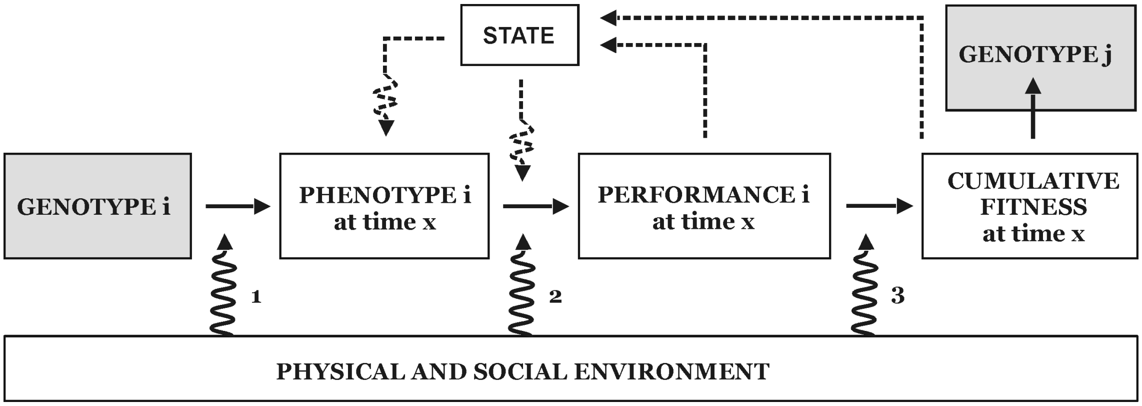
No evolutionary change can occur when all individuals are identical (Darwin 1859). Therefore, the study of individual behavioural variation is essential to gain insight into the adaptive value of behaviour. Evolutionary biologists study how selection affects such phenotypic variation and covariation in natural populations (e.g. Arnold 1983; Lande & Arnold 1983; Bull 1987). A conceptual framework for studying whether selection currently acts upon complex phenotypic traits within a population was developed by Arnold (1983). The rationale is that genetic variation may influence the organism's phenotype (e.g. limb length), which may affect performance (e.g. sprint speed), which in turn can affect fitness (e.g. survival under predation risk). At every step, environmental variation can affect these relationships and ultimately fitness. Dissection of these different steps has been successfully used to study the origins of morphological diversity (e.g. Irschick et al. 2008) and to reveal constraints in morphology and performance (e.g. Vanhooydonck et al. 2001). The inclusion of behaviour in this framework has however proven problematic (Garland & Losos 1994; Irschick et al. 2008; Duckworth 2009), and as a consequence its use in behavioural ecology has been limited (Kingsolver et al. 2001), but see (Dingemanse & Reale 2005).

Three aspects may complicate the analysis of behaviour as a target of selection in this framework. First, behaviour has often been dealt with in discrete categories (e.g. game theory models), describing alternative behavioural strategies/tactics rather than continuous variables (e.g. hawk/dove, Maynard Smith 1982; Sih & Bell 2008). Secondly, evolutionary morphologists and behavioural ecologists may disagree about whether behaviour should be classified as performance or phenotype (e.g. locomotion, Garland & Losos 1994). Finally, behaviour as a target of selection itself differs from morphological measures in that it is highly reactive to the environment (West-Eberhard 1989; Duckworth 2009), and as a result can change with the life-history context of the individual (Houston et al. 1988) and with experience (Dill 1983; Pearce 1997). Nevertheless, the repeatable association between specific behaviours (e.g. hiding) and their selection context (e.g. predator approach), suggests that high reactivity will not prevent individual differences in behaviour to be targets of selection (West-Eberhard 1989).

To take these differences into account, I here expand the original framework by Arnold (1983) in **BOX 1**. It distinguishes behaviour as part of the phenotype (the behavioural repertoire, e.g. personality traits) from behavioural performance (the result of a behaviour in its context), and allows phenotypic traits to change through time depending on the state of the organism. State variables are relatively stable characteristics of the organism that may influence its future expected fitness (Houston et al. 1988). Examples of state variables that are known to affect behavioural decisions are sex (Magurran 1993), size (Johnsson 1993), growth rate (Ruzzante & Doyle 1991), energy reserves (Beukema 1968; Godin & Smith 1988; Gotceitas & Godin 1991) and learned skills (Dill 1983). This approach accommodates recent ideas suggesting that the evolutionary consequences of animal personality need to be viewed in a wider context, exploring associations with phenotypic plasticity (Dingemanse et al. 2010b) and life-history variation (Stamps 2007; Wolf et al. 2007; Biro & Stamps 2008). During the rest of this introduction, I will therefore follow this conceptual framework to set current hypotheses into a broader context and explain the questions addressed in the different manuscripts.

BOX 1
CONCEPTUAL FRAMEWORK FOR THE STUDY OF BEHAVIOURAL (CO)VARIATION

(adopted from Arnold 1983)



In nature, a **GENOTYPE** gives rise to the **PHENOTYPE** (physiology, morphology and behavioural repertoire), that can affect **PERFORMANCE** (the result of a behaviour in its context), which ultimately may affect **FITNESS** (survival and reproduction). Genes, for instance, may act on an individual's aggressiveness, and facilitate it to achieve high social status. Differences in social status may then increase the ability to achieve resources and ultimately growth and fitness (see general conclusions for a discussion of this relationship). Eventually, the strength of these links will affect the representation of genes from GENOTYPE i in the next generation (**GENOTYPE j**). How different nodes correlate depends on the social and physical environment, and gene*environment interactions are likely to occur at every step in this chain:

1 Effects of environment on gene expression
2 Effects of context on performance and use of context-specific information in decision making.
3 Effects of environment on associations between behaviour and its payoffs. Effects of dominance behaviour on resource acquisition can, for instance, depend on the defendability of food in the environment (Grant 1993).

In addition, **STATE**-dependent processes create a link between performance and fitness at an earlier time and the phenotype and performance at present (McNamara & Houston 1986). Possible state variables are e.g. experience, growth strategy, and energy reserves. The **PHYSICAL ENVIRONMENT** entails the distribution of risks and resources in time and space, while the **SOCIAL ENVIRONMENT** denotes the social context, allowing for frequency or density dependent effects. **PERFORMANCE** measures can comprise the avoidance of risks or the acquisition of resources, social status or matings.

Explaining personality

Behavioural consistency

An extreme form of phenotypic consistency can arise when phenotypic traits are largely insensitive to environmental changes, causing firm links between the genotype and phenotype (*environmental canalization*, Waddington 1942). Several personality traits are known to be heritable (van Oers et al. 2005; Réale et al. 2007), and respond to selection (e.g.Johnsson et al. 1996; Sundström et al. 2004). Nevertheless, behaviours are known respond to changes in the environment, to change with experience and through ontogeny (Beukema 1968; Davies 1976; Magnhagen & Staffan 2005; Dingemanse et al. 2010b). Further, if not all individuals respond similarly to the environment, this may affect personality ranks between individuals and disrupt the consistency of behaviour (Réale et al. 2007). Exposure of sticklebacks to a predator not only reduced their aggressiveness but also changed the differences in aggressiveness amongst group members (Bell & Sih 2007). Other personality traits are known to be consistent through the entire lifespan of the individual (Réale et al. 2007). This may indicate that there may be costs involved in changes to personality. Such costs can occur, for instance, when behavioural changes require considerable neuroendocrinological modifications that cost time and energy (Sih & Bell 2008). Other costs can be a direct result of social reinforcement when group structure locks individuals into their strategy (e.g. winner-loser effects, Dugatkin 1997). Similarly, individuals may tend to stick with their previous strategy to avoid errors when information about environmental fluctuations is uncertain (McElreath & Strimling 2006). However, if individuals are constrained to one strategy, why do not all individuals behave the same?

Individual variation

Individual differences can arise when selection pressures on heritable components of behaviour vary across time. In that case, fluctuations in the direction and strength of selection on personality traits may maintain individual variation in behaviour (Bürger & Gimelfarb 2002; Dingemanse & Reale 2005). This is confirmed by observations in wild populations of great tits (*Parus major*) and red squirrels (*Tamiasciurus hudsonicus*) where environmental fluctuations caused changes in both the direction and strength of selection on personality traits (Dingemanse et al. 2004; Boon et al. 2007; Quinn et al. 2009). Alternatively, variation can be maintained because the fitness of a trait depends upon its frequency in the population (*frequency-dependent selection*, Clarke &

O'Donald 1964). Minnows (*Phoxinus phoxinus*), for instance, show substantial individual variation in risky predator inspection behaviour (Magurran 1986) and a model by Dugatkin and Godin (1992), predicts that the individual fitness associated with predator inspection depends on the frequency of the behaviour in the population. Similarly, aggressive strategies such as *hawk-dove evolutionary games* (Maynard Smith 1982) and innovative behaviour (*producer-scrounger*, Vickery et al. 1991) are frequency dependent. Although such patterns can arise by selection on heritable traits, plastic responses along with individual differences in experience with the physical or social environment can generate similar patterns of individual variation in behaviour (McElreath & Strimling 2006; Wolf et al. 2008). Experienced individuals may, for instance, have better predator inspection skills, suffer less risks during inspection and, as a consequence, be more prepared to approach a predator. However, why would such differences in personality affect groups of behaviours rather than separate behaviours?

Behavioural syndromes as a functional constraint

When different personality traits are measured simultaneously, theory predicts a negative correlation between the performance of different behaviours due to time budget conflicts (Sih et al. 2004b) and limited attention (Dukas 2002). Time budget conflicts occur when behaviours cannot be performed simultaneously, leaving individuals a limited amount of time to perform a single behaviour, thereby reducing the opportunity to carry out others (Sih et al. 2004b). Likewise, an animal may not be able to forage and hide from a predator simultaneously (Milinski & Heller 1978; Sih 1980; Lima & Dill 1990). Effects of limited attention are likely to enlarge the impact of time budget conflicts on performance when more complex behaviours are involved (e.g. courtship, foraging and predator vigilance). Limited attention is a general description of constraints to the amount of information per time unit that can be processed by the brain (Dukas 1999; Attwell & Gibb 2005) that reduces the capacity to perform behaviours simultaneously. For example, individuals of a small South American cichlid fish, *Nannacara anomala*, have more difficulty detecting predators when involved in agonistic interactions (Jakobsson et al. 1995; Brick 1998; Brick & Jakobsson 2002). Because time budget conflicts result in a negative association between the intensity of different behaviours, they generate tradeoffs between these behaviours. Behavioural syndromes, on the contrary, generally represent positive associations between the intensity of active behaviours (Sih et al. 2004b).

A possible explanation for the occurrence of stable positive correlations between different behaviours is that they share relatively static common mechanisms (*constraint hypothesis*, Sih et al. 2004a; Bell 2005). Mechanisms suggested to cluster behaviours in behavioural syndromes like this are pleiotropic gene effects, hormones or experiences that steer the intensity of different behaviours simultaneously. Evidence for genetic correlations between different behaviours in a variety of species to some extent supports this view (Sluyter et al. 1995; van Oers et al. 2004; Bell 2005; Galsworthy et al. 2005; Quinn et al. 2009). In German shepherd dogs for instance, boldness and aggressiveness are genetically correlated. Therefore selection on either behaviour will have marked effects on the other (Strandberg et al. 2005). Several hormones act on suites of correlated personality traits rather than on single behaviours, suggesting possible neuroendocrinological mechanisms behind genetic correlations (Koolhaas et al. 1999; Martins et al. 2007; Overli et al. 2007). A testable prediction arising from the constraint hypothesis is that behaviours which are part of a behavioural syndrome cannot respond independently to changes in the environment or selection.

Adaptive behavioural syndromes

Alternatively, if behavioural syndromes vary between populations subjected to different selection pressures, this can be interpreted as indicators of local adaptations (*adaptive hypothesis*, Wilson 1998; Bell 2005). Syndromes may therefore reflect genetic correlations among behavioural traits that work well together in nature (Stearns et al. 1991). Studies on three-spined sticklebacks support this hypothesis, where phenotypic and genetic correlations differ between populations (Bell & Stamps 2004; Bell 2005; Dingemanse et al. 2007; Brydges et al. 2008). Further, syndromes are more common in predator-sympatric populations, suggesting a role for predation in shaping associations between behaviours (Bell 2005; Dingemanse et al. 2007). Additional investigation demonstrated that a combination of correlated selection and behavioural plasticity in response to trout predation generated a previously absent correlation between boldness and aggression in a population of sticklebacks (Bell & Sih 2007).

Personality and behavioural syndromes as a result of inner state?

Recent theoretical studies have suggested a novel adaptive scenario to explain behavioural consistency (Dall et al. 2004; McElreath & Strimling 2006; Stamps 2007; Wolf et al. 2007). The idea is that individual variation in state can, in combination with frequency dependent selection (Dall et al. 2004) or life-history tradeoffs (Wolf et al. 2007), result in behavioural syndromes. Individuals prioritizing growth, for example, should be more keen to take risks during foraging and to engage in agonistic interactions to compete for food (Stamps 2007; Biro & Stamps 2008). Stable individual differences in growth rate (*intrinsic growth rate*) have been demonstrated in a wide variety of animals (Brown 1946; Arendt 1997; Mangel & Stamps 2001; Ragland & Carter 2004; Johnsson & Bohlin 2006), and suggest that growth may be a key variable when investigating ultimate questions about animal personality in nature. A critical assumption to this hypothesis is that risk-prone behaviour correlates positively with growth or reproduction, a prediction that few studies have tested in the wild (Biro & Stamps 2008).

Interestingly, several studies suggest that patterns of covariation in life-history traits are similar to those observed between behaviours (Promislow & Harvey 1990; Reznick et al. 2002; Ricklefs & Wikelski 2002). In birds, for instance, life-history strategies within and among populations group into a slow-fast continuum with slow development, low reproductive rate and long lifespan at one end and the opposite traits on the other (Ricklefs & Wikelski 2002; Ricklefs & Scheuerlein 2003). Also from this angle, state variables affecting expectations of future reproduction have been suggested to affect life-history traits and suites of morphological, physiological and behavioural traits linked to these (Ricklefs & Wikelski 2002). As a result, individuals appear to respond to environmental stressors or perceived risks with changes to their life-history traits. Changes are however not without costs, and augmented rates of somatic growth are shown to be associated with higher rates of mortality (Johnsson & Bohlin 2006; Dmitriew & Rowe 2007).

Brown trout (*Salmo trutta* L.) as a model species

My studies use juvenile life stages of brown trout (*Salmo trutta*) as model species. Brown trout is a common fish species in European streams and has been introduced to many other continents (Elliott 1994). Although life cycle patterns can vary between populations, the populations used in this thesis are largely anadromous and individuals develop in the stream before migrating downstream to the sea, generally at age 2 (Bohlin et al. 1994). In what follows, I refer to different juvenile age classes as fry for juveniles less than 6 months of age, and parr for juveniles between 6 months and the onset of migration as smolt.

Brown trout is a good model species to study questions about behavioural ecology. First, they show extensive variation in behavioural and life-history patterns. Ferguson & Mason (1981), for instance, showed that a single lake in north-western Ireland (Lough Melvin) contains at least three genetically separated types of brown trout, differing so much in foraging habits and morphology that they all received their own local name. Individual differences in behaviour also occur within the same genetic pool, and individuals from the same population are shown to differ in aggressive (Lahti et al. 2001; Höjesjö et al. 2002), risk-taking (Sundström et al. 2004; Brelin et al. 2008) and foraging strategies (Ringler 1985). Also life-history strategies can be variable within trout populations, resulting in differences in growth, reproductive or migratory life-history (Dellefors & Faremo 1988; Bohlin et al. 1994; Johnsson & Bohlin 2006). State variables such as body size or growth have further been linked to variation in trout risk- taking and agonistic behaviour in laboratory experiments (Johnsson et al. 2006), suggesting that they can also play a role in nature.

BOX 2

TROUT AND RESTOCKING PROGRAMS

The use of trout as a model further adds an applied aspect to this thesis. Some brown trout populations currently suffer from environmental degradation and overfishing. Thereby, river regulation by damming generates a well-known problem for smolt and adult migration, resulting in habitat fragmentation or local extinction of populations (Dynesius & Nilsson 1994). Countries around the Baltic sea currently maintain breeding programs that release close to four million hatchery produced brown trout smolt per year (ICES 2009). Despite this major effort, estimates still show a steady decline in wild occurring stocks since the mid 1990s (ICES 2009). The value and efficiency of these hatchery release programs is therefore debated, and several studies confirm a lower fitness of hatchery trout in nature in comparison with wild trout (reviewed in Araki et al. 2008).

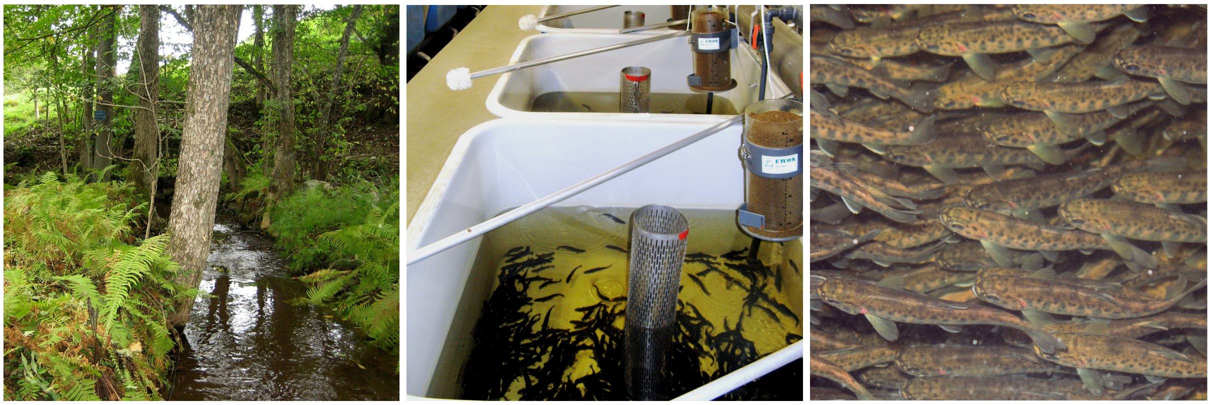


Figure 2 Hatcheries differ strongly from wild habitats in that they contain little (variation in) physical structure, high densities of conspecifics, plenty of food and no predation risks. **left**: a natural trout habitat (Stenungeån), **middle**: hatchery tanks at the former Swedish Board of Fisheries research station, Kälarne, Sweden, **right**: fry in a high density treatment in paper **II**.

Differences between hatchery and wild salmonids can arise through four processes. *First*, directional selection for preferred traits in the hatchery, such as fast growth, may influence several phenotypic traits in concert. Hatchery selection for example causes trout to accept higher predator risks (Johnsson et al. 1996; Sundström et al. 2004). S*econd*, wild salmonids invest considerable time in mate choice, whereas artificial propagation methods in a hatchery leave few opportunities for sexual selection to occur (Wedekind 2002; Fraser 2008). Little is known about the effects of the disruption of sexual selection processes in captive breeding programs, nevertheless, several studies suggest this can severely impact offspring health (Wedekind 2002). *Third*, the safe hatchery environment results in a considerably higher survival (more than 85%) compared to the wild (less than 10%, McNeil 1991; Elliott 1994; Reisenbichler & Rubin 1999). Thus, natural selection is relaxed in the hatchery environment. *Fourth*, differences between the natural and hatchery rearing environment may lead to different phenotypic development in salmonids with the same genetic background (**Figure 2**). In response, hatchery reared trout are shown to differ from wild trout in several aspects of their behaviour and often show higher risk-taking behaviour towards predators, aggression and foraging motivation, suggesting that hatchery rearing does not provide fish with the skills needed for survival in nature (Einum & Fleming 2001; Huntingford & Adams 2005).

AIMS OF THE THESIS

The overall aim of this thesis is to improve the understanding of the causes and consequences of behavioural variation in brown trout (*Salmo trutta*). More specifically I explored the following aspects:

1) To what extent is variation in behaviour consistent within and across contexts?
(**papers I, III & IV**)

2) How do genetic and environmental variation affect behaviour?
(**papers I, II & III & IV**)

3) How does this affect performance in the wild?
(**papers I, II, IV & V**)

4) Whether this understanding can be used to improve rearing methods of supplementary hatcheries?
(**papers II & III**)

METHODOLOGY

Experimental fish & breeding setups

All experiments were carried out with juvenile freshwater life stages of brown trout (*Salmo trutta*). I used wild caught individuals from natural populations (**papers III & IV**) as well as hatchery reared offspring from wild caught individuals (**I & III**) or sea-ranched individuals (**II**). Sea-ranched trout are generally reared in a hatchery from egg to smolt stage before they are released in natural streams. This is a common practice in release efforts to compensate for declines in natural brown trout populations in Sweden (Pettersson et al. 1996). In three studies (**I, II & III**), hatchery breeding setups were used to control for the inheritance or the environment during development of the studied individuals.

In the first experiment (**I, Figure 3**) parents of experimental fish were wild caught from River Norumsån on the Swedish west coast (latitude 58°N). In this population, migration life-histories are known to vary between individuals (*partial migration*, Lack 1943). A varying proportion of individuals, often males, adopt a stationary life-history strategy while the rest migrate to sea when reaching the age of two (Dellefors & Faremo 1988). In order to test if migratory strategy affected offspring behaviour, one migratory and one stationary father were crossed to each female (*nested full-sib, half-sib breeding design*, see Johnsson et al. 1993; Vollestad & Quinn 2003). Following fertilization, the eggs were moved to E. ON fish farm in Laholm (Sweden) and incubated in hatchery tanks until the start of the experiments (age 1 month).

In **paper II**, I tested for effects of altered rearing conditions (density and physical structure, **Figure 4**) on the development of behaviour in trout of similar genetic background. Sea-ranched parents were obtained from river Dalälven (latitude 60°N, for strain information see Johnsson et al. 1996). 11 males and 11 females were paired and the eggs of each female were artificially fertilized with the milt of one male following standard hatchery procedures. Eggs were pooled and randomly distributed among hatchery tanks (1×1 m^2) in three density treatments: conventional hatchery density (2500 individuals/m^3), approximately a fourth of conventional hatchery density (600 individuals/m^3) and natural density (150 individuals/m^3, Elliott 1994). Further, we added structural complexity in half of the tanks. Structure consisted of plastic bags,

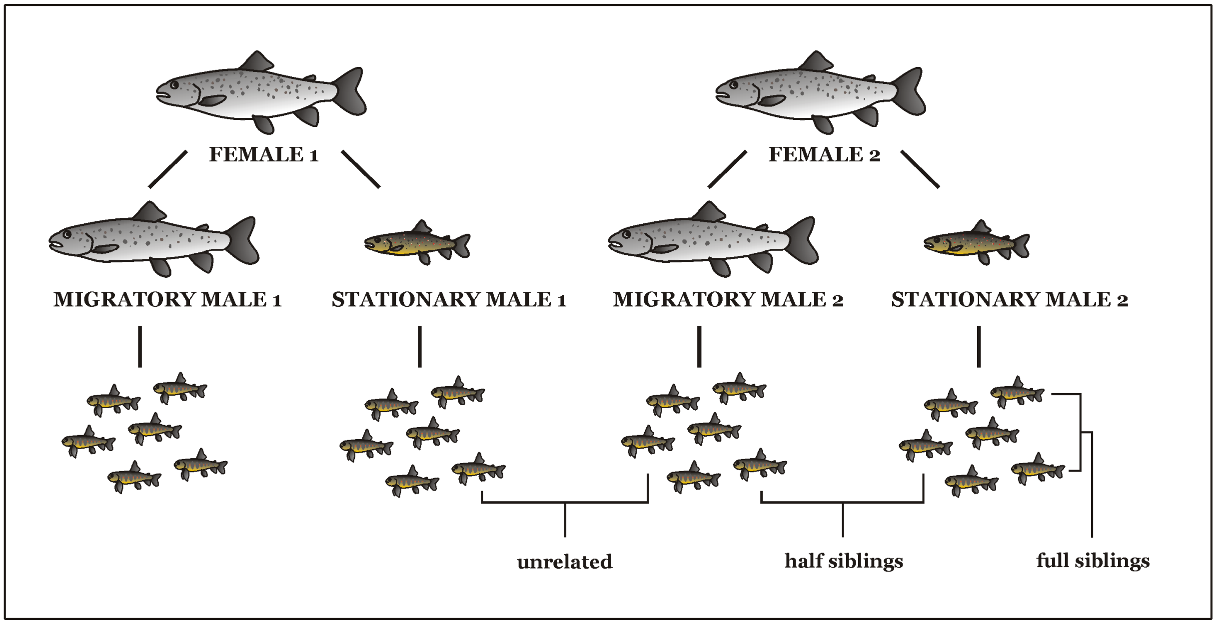


Figure 3 Maternal full-sib, half-sib breeding setup used in **paper I**. Each female was mated with one male with migratory and one with stationary life-history. A total of 9 females and 18 males were used, resulting in 18 families.

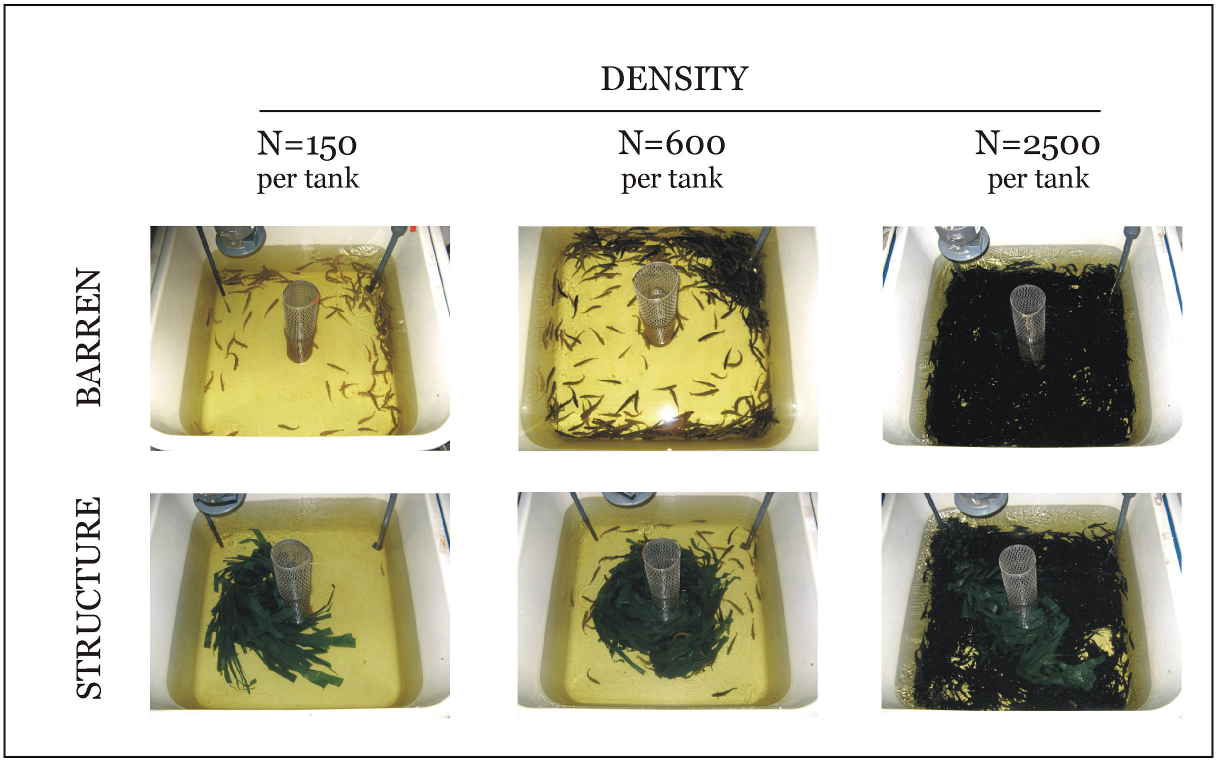


Figure 4 The setup used in **paper II**. Eggs from crosses between 11 females and 11 males were mixed and randomly distributed between a total of 24 hatchery tanks in one of six combinations of density and structure treatments.

sliced up to resemble water-plants and provided with a stone ballast to keep them in place. This provided fish with physical refuge, more heterogeneous water flow dynamics and increased visual isolation between individuals compared with the barren tanks. We conducted experiments with fry (age 3 months) and parr (age 6 months) from these different treatments.

In two studies, wild parr yearlings were caught by electric fishing from naturally reproducing populations of brown trout on the Swedish west coast (latitude 58°N): in river Norumsån (age 6 months, **III**) and Stenungeån (age 1+ y, **IV**). In paper III the behaviour of wild caught and hatchery reared parr (from the breeding setup in **paper I)** was compared.

To reduce sampling bias in nature (Wilson et al. 1993; Satterlee & Jones 1997), stream sections were fished repeatedly, and a random sample of individuals was selected within a pre-set size range. When a subset of fish was selected from laboratory tanks (**I & II**), the sampling procedure was adjusted to minimize sampling bias from stock tanks. The water level in holding tanks was first lowered before a net was rapidly moved twice from side to side in the tank. The sample was then transferred to a bucket filled with water and fish were again netted, but now diagonally from bottom to top. This procedure was repeated three times until a sufficient number of fish were sampled.

Laboratory methods

In collaboration with my co-authors, I measured different behavioural traits in individual fish. Depending on the experimental design, behaviours were recorded manually (**I to IV**), with event recording software (Observer, Noldus: **III** and JWatcher: **II & IV**) or with a video camera (**II**). Behaviour and space use of brown trout tend to vary with age and size (Huntingford & Turner 1987). Behavioural traits were therefore selected following observations of behavioural motivation in pilot observations. We measured the following behavioural traits:

1) *Aggressiveness* describes an individual's agonistic reaction towards conspecifics (Huntingford & Turner 1987). We measured the response of fry to their own mirror image (Gallup 1968, **I**) and the response of parr to an intruder of standardized length (**IV**).

2) An individual's *response to novelty* is a function of its boldness or exploration tendency (Wilson et al. 1993; Réale et al. 2007). Whereas currently no general consensus exists about the difference between these personality traits, we follow a broad definition of boldness (Wilson et al. 1994) as the individual's response to any situation that entails a certain risk or novelty (e.g. a novel object, novel food, novel environment or a predator). Different from Réale et al. (2007), we do not consider exploration behaviour in a novel environment a separate personality trait in brown trout, but rather a more specific measure of boldness (to a novel environment). This likely corresponds to the ecology of juvenile brown trout, which generally respond with a certain care to disturbance or changes to the environment (Elliott 1994). I used three measures of boldness. 1) The response to *novel prey*: brine shrimp (**I**) or liver and a live maggot (**II**). 2) The exploration of a *novel environment*: a maze (**III**) and/or a novel foraging area (**III & IV**). And 3) the response of fry to a *novel object* (a washer, ∅ 12mm, **I**).

3) In **papers III & IV**, the ability of trout to *forage on a cryptic prey* (familiar) was observed in a setup modified after Johnsson and Kjällman-Eriksson (2008). Trout are visual predators that mainly forage on invertebrate prey in drift and on the bottom of the river (Bridcut & Giller 1995; Rincon & Lobon-Cervia 1999; De Billy & Usseglio-Polatera 2002). When prey are cryptic, foraging requires visual acuity, for instance the capacity to discriminate between subtle colour differences and detect small movements (Lythgoe 1979).

4) Another cognitive foraging task, *maze search*, was scored in **papers II & III**, where I measured food search behaviour in a maze. In **paper III** we used a two-armed maze adopted from experiments with groups of minnows (Figure 1 in **III**, Johnsson & Sundström 2007). Maze search performance of brown trout in this setup was however poor, and I exchanged this setup in further experiments with a four armed maze (Figure 1b in **II**). Food search behaviour in these experiments is an estimate of the ability of the fish to use olfactory and visual cues to orientate itself in a structured environment.

5) Individual differences in *habitat choice* were measured in **paper III**, where trout were given the choice between a structured and an open half of an experimental tank.

To evaluate the repeatability of behaviour and effects of learning, foraging and exploration behaviour in the maze and/or cryptic prey task were measured repeatedly for the same individuals across different trials (**III & IV**). Both cryptic prey foraging and maze search likely represent a cognitively demanding task for brown trout. The presence of a hidden food reward further allows for flexible responses in activity and prey search patterns with increasing experience in these setups through learning (Brown et al. 2006). Similarly, aggressiveness was scored twice and analyzed for repeatability (**IV**). I further tested for behavioural syndromes by comparing behaviour of the same individuals across different contexts in **papers I, III and IV**.

In addition, I determined dominance status in pairs of fry (dyadic contest, **I**) and groups of parr (serial removal experiment, **IV**). To enable recognition of individuals during these observations, fish were marked by adipose fin clipping (**I**) or attaching a coloured pearl tag to their dorsal fin.

Methods in the field

In the field, I used electrofishing to capture fish for experiments (**I, III & IV**) and to recapture fish after release (**I, II & IV**) following methods outlined by Bohlin and colleagues (1989, LUGAB 1000, straight DC, 200-400V for **papers I, III & IV**, 1000-1200V for **II**). Fish were released at the position they (**IV**: river Stenungeån, latitude 58°N), or their parents (**I**: river Norumsån, latitude 58°N) were caught. In **paper II**, fish were released into an experimental section of river Aneråsån that is enclosed with a metal grid (Latitude 62º N). No fish could therefore escape or invade this stream section. Predators sighted in and around these three streams are heron (*Ardea cinerea*, all rivers), mink (*Mustela vision*, all rivers), otter (*Lutra lutra*, only Aneråsån), and resident trout (only Stenungeån and Norumsån).

In order to recognise fish after release (**papers II & IV**) they were provided with a passive integrated transponder tag into the peritoneal cavity (PIT ID100, Trovan Ltd, Roussel et al. 2000). Length of fry used in **paper I** was below the lower limit for using PIT tags. We therefore clipped the adipose fin of each individual before release and performed parentage analysis on fin samples of recaptured fin-clipped individuals (O'Connell & Wright 1997). Variation on eleven polymorphic microsatellite DNA loci was used to assign individuals to the correct full-sibling group.

Juvenile brown trout are very stationary, and seldom move further than 100m from the release point (Bohlin et al. 2002). To further increase the possibility to catch dispersed individuals, stream sections in Norumsån and Stenungeån were fished at least 130m downstream and 130m upstream from the location of release. To ensure high recapture rates we performed three removals with a 30min time interval (Bohlin et al. 1989). In Aneråsån, removals were repeated until three subsequent fishing bouts yielded no fish (in total 7 bouts), ensuring that no fish remained in the river section. Recapture rates in our experiments therefore should be a good proxy for survival.

Statistical methods

The quickly emerging research field of animal personality and behavioural syndromes has generated some new statistical approaches to study covariation in behaviour (Bell 2007; Dingemanse et al. 2010a; Dingemanse et al. 2010b; Dochtermann 2010). I will in this paragraph outline some issues that make data analysis different from other studies in behavioural ecology and how I dealt with these in my experiments.

Behavioural syndromes or personality are typically analysed with correlation methods (Sih & Bell 2008). This however inevitably generates a large number of correlations which increases the probability to falsely identify associations (Type I error, Quinn & Keough 2002). Therefore I chose to report original significance values alongside solutions that account for multiple testing errors. Bonferroni corrections of significance values offer a first solution to this problem by minimizing the chance of making type I errors (Rice 1989). In **paper IV**, type I errors were reduced with sequential Bonferroni correction (Rice 1989). The use of this correction method has nevertheless been criticized because it can lead to a greater risk to falsely reject genuine correlations when the number of tests is large (Type II error, Moran 2003). Several studies have therefore recently implemented the use of false discovery rate (FDR) to adjust for multiple testing errors in this context (Conrad & Sih 2009; Logue et al. 2009; Dochtermann 2010). I followed this procedure in **papers I & III** following methods outlined by Benjamini & Hochberg (1995, see also Verhoeven et al. 2005).

When behavioural traits grouped into logical clusters after exploratory correlation analysis, I used principal component analysis (PCA, Logue et al. 2009)) to summarize behaviours into a smaller amount of logical categories or principal components (PC, **I, III & IV**). PC were used in further analyses and referred to by their number or by the behavioural category they describe. In this, the first PC (PC1) describes the major axis of behaviour, while any further PC describes an ever smaller part of the remaining variation in the variables.

In **paper IV**, I used linear mixed effects modelling (LMM) to estimate individual consistency in behaviour over trials (random regression analysis, Pinheiro & Bates 2000; Dingemanse et al. 2010b),). In contrast to other methods for assessing behavioural consistency (Lessells & Boag 1987), LMM takes into account changes to the mean value across trials that can arise due to, for example, habituation effects or learning (Hayes & Jenkins 1997; Dingemanse et al. 2010b). LMM also allows for the addition of fixed effects that may bias measures of behaviour and test for their contribution in affecting variation. Individual estimates of random effects, accounting for significant fixed effects, can be extracted from such models in the form of best linear unbiased estimates (BLUP, Henderson 1975). I used this latter approach to estimate individual scores of foraging activity and aggressiveness and behavioural change in foraging activity over trials in **paper IV** (exploration, aggressiveness and behavioural flexibility respectively). Some recent papers have critizised the use of BLUP to infer breeding values (Hadfield et al. 2010; Wilson et al. 2010b). We stress, however, that BLUP were not used as a method to estimate genetic components of behavioural variation, but rather to estimate family or individual values for behaviour while accounting for significant fixed effects.

SHORT SUMMARY OF EACH PAPER

I Höjesjö J, Adriaenssens B, Bohlin T & Johnsson IJ. Behavioural syndromes in juvenile brown trout (*Salmo trutta*); life-history, family variation and performance in the wild.

The aims of this study were to investigate (1) the occurrence and strength of the shyness-boldness behavioural syndrome in brown trout fry, (2) whether this syndrome is associated with paternal migratory life-history, (3) whether fry survival and growth in the wild is associated with paternal life-history and/or boldness, and (4) whether offspring performance showed maternal effects. Nine female migratory trout were each crossed with one migratory and one stationary male and the offspring were raised in hatchery tanks until the onset of first feeding (age 1 month, **Figure 3**).

Fry showed high variation in their response to a novel object, a novel prey and in aggression towards their mirror image. Furthermore, individuals showed consistent differences in behaviour across these three functional contexts, representing a behavioural syndrome. Hence, fry that responded bold towards a novel object also accepted a novel food item earlier and responded more aggressively towards their own mirror image. This is consistent with previous work identifying a shy-bold syndrome in a range of species (Wilson et al. 1994). Principal component analysis resulted in one component describing this major axis of variation in boldness which accounted for 34% of the behavioural variation (PC1). Deviations from this shy-bold syndrome (PC2), where less aggressive individuals performed more approaches to the food explained an additional 17% of the behavioural variation. Fry growth and survival in the wild was not associated with boldness (PC1) nor PC2, suggesting that several behavioural strategies can yield similar fitness in brown trout fry.

Paternal migratory life-history influenced PC2, but not the major axis of offspring boldness. Significant effects of the female parent on both boldness and body size suggested however maternal and/or genetic effects. Other studies have shown genetic effects on agonistic and risk-taking behaviour in salmonids (Riddell & Swain 1991; Sundström et al. 2004). However, effects of the maternal environment might have been more important than genetic effects in our study (Falconer & Mackay 1996). Effects of female parents on fry size further persisted over the first growth period in the wild, which may have implications for fitness during early life.

II Brockmark S, Adriaenssens B & Johnsson JI. Less is more: density influences the development of behavioural life skills in trout.

In this study we predicted that reduced rearing density and increased structural complexity promote the development of life skills in brown trout. To test this, we randomly distributed eggs from crosses between 11 males and 11 females among 24 tanks in one of six combinations of density and structure treatments as outlined in **Figure 4**. We conducted the experiments with fry (age 3 months) and parr (age 6 months) from these different treatments.

The results show that reduction of rearing density substantially improves foraging and anti-predator skills in young brown trout. As a result, fry from natural densities developed better food search skills in a maze, and parr reared at natural density ate novel prey sooner and escaped more efficiently from a simulated predator attack. Parr reared at reduced densities were also twice as likely to survive in nature as parr reared at high density. Two processes may have impaired the development of individual behaviour at high densities. First, sensory overload caused by crowding in combination with restriction in movement and perception may constrain the development of both social and individual behaviour (Dukas 2002). Alternatively, rearing conditions may alter the trade-off between the use of private or public information in behavioural decisions (van Bergen et al. 2004; Kendal et al. 2005). Development at high densities, where private information is difficult to gather, may thus favour the use of public information and over time lead to conformity through more or less irreversible losses of the ability to make individual decisions (Couzin et al. 2006).

Effects of structure were less clear-cut, and actually reduced escape performance of trout parr. These results show that more nature-like rearing densities may facilitate the development of behavioural skills in captive animals, thereby increasing their contribution to natural production. In this, a reduction in rearing density resulted in more bold foraging behaviour together with better predator escape skills and survival upon release.

III Adriaenssens B & Johnnson JI. Learning and context-specific exploration behaviour in hatchery and wild brown trout.

In this study I investigate whether rearing environment (wild vs. hatchery) affects the ability of brown trout parr to learn two foraging tasks. In addition, I examine whether exploration behaviour in trout is a general personality trait, consistent across different situations, or situation-specific. Hatchery- and wild-reared brown trout parr (age 6 months) were trained in two different foraging tasks: locating food hidden in a maze and finding a cryptic prey, and their performance within and across tasks was compared.

I observed no learning in the maze task, whereas trout reduced their search time for cryptic prey by learning. Hatchery trout were more successful foragers in both tasks and learned faster than wild trout when foraging on cryptic prey. This differs from most previous studies which suggested reduced foraging skills in hatchery reared salmonids (e.g. Sundström & Johnsson 2001).

Exploration behaviour of brown trout was highly consistent within both tasks, illustrating personality. However, individuals adjusted their behaviour to the context, and trout scored as fast explorers in the maze did not necessarily behave likewise in the cryptic prey task. Exploration tendency was therefore best explained as a context-specific trait. Evidence from other animal species suggests that selection can result in both context-specific (Coleman & Wilson 1998) and general behavioural syndromes (Huntingford 1976). The same behavioural syndrome structure described exploration behaviour for hatchery and wild trout. However, wild trout were more consistent than hatchery trout in their exploration strategy. Such differences could be caused by the rearing environment per se or by natural selection against individuals with less consistent behaviour in the wild-reared trout.

IV Adriaenssens B & Johnsson JI. No favors for the reckless: do personality traits predict fitness of brown trout in the wild?

Studies on the association between personality traits and fitness related measures in nature are rare. Here I tested for associations between three behavioural axes in wild brown trout parr (age 1+ year): exploration tencency, behavioural flexibility and aggressiveness. Next I studied how these individual behaviours relate to social dominance and performance under natural conditions (growth, survival and movement).

Our results support a behavioural syndrome in brown trout with more explorative individuals being more aggressive and showing more flexible behaviour. None of these behaviours affected social status, and aggressiveness and social status were poor predictors of performance in the wild. Interestingly, however, slow exploring personality types grew faster than bolder conspecifics in the wild. The finding that shy behaviour can result in faster growth in nature challenges the view that personality traits can be predicted by constant associations with life-history tradeoffs (Biro & Stamps 2008).

V Adriaenssens B & Johnsson JI 2009. Personality and life-history productivity: consistent or variable association?

The occurrence of animal personality in nature is not easily explained (Sih et al. 2004a; Dingemanse & Reale 2005). Biro and Stamps (2008) defend the compelling hypothesis that consistent individual variation in behavioural traits can be explained by associations with traits involved in life-history tradeoffs. Such associations would favour personality traits when individuals differ consistently in rates of biomass production through growth or reproduction. In response to this article, we point out that associations between personality traits and life-history productivity may be more common in homogeneous (e.g. captive) environments, where directional selection can result in more stable associations between personality and life-history productivity. In contrast, more variable associations are expected in nature because of complex interactions between environmental heterogeneity and behavioural payoffs. This view is further supported by the results in **paper I, II and IV**, showing that associations between boldness and growth in the wild are difficult to predict.

MAIN FINDINGS

- I show evidence that behavioural variation in brown trout often associates into behavioural syndromes. ***Separate behaviours of brown trout can therefore not be considered as isolated units***, but often combine into clusters.

- ***Behavioural variation was influenced by a combination of inherited and environmental effects.*** First, individuals from different maternal and paternal origin differed in their aggressiveness and response to novel prey or novel food. (**I**). Secondly, reduced rearing densities increased the response to novel prey, food search ability in a maze and predator response (**II**). Third, hatchery trout were more successful foragers than wild conspecifics, yet showed less repeatable exploration behaviour across time (**III**).

- ***Reduced hatchery rearing densities facilitate the development of adaptive behaviour and post release survival in brown trout.*** These finding suggests that reduced rearing densities can promote the development of life skills in captive animals and may have implications for current rearing methods in supplementary hatcheries (**II**).

- Personality traits were generally poor predictors of growth and survival upon release, suggesting that several behavioural strategies can be successful in nature. However, in **paper II** efficient foragers with superior anti-predator behaviour survived better upon release, whereas in **paper IV** slow exploring individuals grew faster than more bold trout. ***This contradicts a simple association between risk taking behaviour and growth-mortality tradeoffs under natural conditions.***

GENERAL CONCLUSIONS

Advice for hatchery rearing

Most captive rearing programs of fish aim at providing fish for the food marked (Brännäs & Johnsson 2008). Parallel to this, hatchery breeding programs also breed fish to compensate for declines in wild salmonid populations (ICES 2009). Whereas rearing methods in supplementary hatcheries are at present very similar to those in intensive fish farms, they may require very different approaches to reach their goals (Brännäs & Johnsson 2008). Several studies now show that hatchery reared fish differ phenotypically from wild fish and that this often impairs their survival in nature and the health of wild stocks (Olla et al. 1998; Einum & Fleming 2001; Araki et al. 2008). Pre-release training of behavioural skills has been put forward as a solution to this problem, yet results have been mixed (reviewed in Brown & Laland 2001). Our results, on the other hand, indicate that a simple change (reduction of rearing densities) can promote the development of behaviour in hatchery salmonids. In addition, we show that trout reared at lower densities are twice as likely to survive their first month after release compared to trout reared at higher densities. Changing focus from quantity to quality of released fish may therefore improve the efficiency of release programs. To evaluate the feasibility of this approach, further studies need to investigate whether higher adult return rates compensate for the increased production costs of low density rearing. In addition, concerns about the ethical aspects of captive rearing programs become increasingly important in decisions of whether we are prepared to pay this higher cost (Shumway 1999; Ashley 2007).

Personality and growth-mortality tradeoffs

Theoretical discussions recently suggested that personality may be a consequence of strong associations between behaviour and an individual state (see **BOX 1**, Wolf et al. 2007). Associations with a relatively stable state variable may then cause several behaviours to be consistent across time (personality) and show associations amongst one another (behavioural syndrome). Stable individual differences in growth rate have now been proposed as a state variable favouring the evolution of personality (Stamps 2007; Biro & Stamps 2008). As a result of growth-mortality tradeoffs, individuals prioritizing growth should then be more keen to take risks during foraging and more aggressive in competition for food. As discussed in **paper V**, I suggest that this hypothesis may underestimate the complexity of associations between growth and personality traits in nature.

The occasional absence of correlations between bold behaviour and growth in natural populations has previously been explained by reduced predation risks (Fraser et al. 2001; Biro et al. 2004), an environmental variable with obvious links to growth-mortality tradeoffs. In **paper V**, however, we suggest that also other aspects of the environment affect payoffs of personality traits. Such include the density of competitors and resources and their distribution in space and time (Grant 1993). Positive associations between aggression and food intake rates thereby typically occur in simple, predictable environments but often break up when the environment becomes more complex (e.g. Pettersson et al. 1996; Sundbaum & Näslund 1998; Hofmann et al. 1999; Sloman & Armstrong 2002; Höjesjö et al. 2004; Sneddon et al. 2006).

In agreement with this, our results show that personality traits of brown trout are generally poor predictors of their growth rate or survival in complex, natural environments (**I, II & IV**). In **paper IV**, however, we found slow exploring individuals to grow faster than more bold trout. Our results are likely the first to report a negative correlation between risk-prone personalities and growth rate in the wild. However, in several species, the growth of offspring from more bold mothers has been found to be slower when compared shy mothers (Both et al. 2005; Boon et al. 2007; Wilson et al. 2010a). Other studies have also shown more heterogeneous, and often negative, associations between bold behaviour and mortality in nature (e.g. in bighorn sheep, *Ovis Canadensis*, Réale & Festa-Bianchet 2003 and Reale et al. 2009; reef fish, *Pomacentrus amboinensis*, Meekan et al. 2010; great tit, *Parus major*, Dingemanse et al. 2004 and Quinn et al. 2009). Together, these results suggest that links between behaviour (i.e. risk-taking behaviour), and growth and mortality may be more variable under natural conditions (Lind & Cresswell 2005).

More study is needed to distinguish the exact mechanisms that cause this variation. Analysis of these mechanisms may require a closer look at under which conditions energetic costs outcompete foraging benefits of alternative behaviours (Grant 1993). Grant and Noakes (1988), for instance, show that differences in water current can change the costs of active movement in stream-living fish, and influences their aggressive tactics. Moreover, also changes in the social environment (Metcalfe 1986; Vollestad & Quinn 2003), or physiology (Cutts et al. 1998; Monclús et al. 2005; Stoks et al. 2005; Millidine et al. 2009) may interact with the net benefits of behaviours. This suggests a greater importance of fluctuating selection pressures in explaining variation in personality traits in nature (see e.g. Wilson et al. 1994; Dingemanse et al. 2004). Future studies should therefore take variable associations between environmental variation and state variables into account to generate a more complete image of the evolutionary processes that maintain behavioural syndromes.

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REFERENCES

Araki, H., Berejikian, B. A., Ford, M. J. & Blouin, M. S. 2008. Fitness of hatchery-reared salmonids in the wild. *Evolutionary Applications*, **1**, 342-355.

Arendt, J. D. 1997. Adaptive intrinsic growth rates: an integration across taxa. *The Quarterly Review of Biology*, **72**, 149-177.

Arnold, S. J. 1983. Morphology, performance and fitness. *American Zoologist*, **23**, 347-361.

Ashley, P. J. 2007. Fish welfare: current issues in aquaculture. *Applied Animal Behaviour Science*, **104**, 199-235.

Attwell, D. & Gibb, A. 2005. Neuroenergetics and the kinetic design of excitatory synapses. *Nature Reviews Neuroscience*, **6**, 841-849.

Bell, A. M. 2005. Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of Evolutionary Biology*, **18**, 464-473.

Bell, A. M. 2007. Future directions in behavioural syndromes research. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 755-761.

Bell, A. M., Hankison, S. J. & Laskowski, K. L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771-783.

Bell, A. M. & Sih, A. 2007. Exposure to predation generates personality in threespined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, **10**, 828-834.

Bell, A. M. & Stamps, J. A. 2004. Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, **68**, 1339-1348.

Benjamini, Y. & Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**, 289-300.

Beukema, J. J. 1968. Predation by the three-spined stickleback (*Gasterosteus aculeatus* L.): the influence of hunger and experience. *Behaviour*, **31**, 1-125.

Biro, P. A., Abrahams, M. V., Post, J. R. & Parkinson, E. A. 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 2233-2237.

Biro, P. A. & Stamps, J. A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, **23**, 361-368.

Bohlin, T., Dellefors, C. & Faremo, U. 1994. Probability of first sexual maturation of male parr in wild sea-run brown trout (*Salmo trutta*) depends on condition factor 1 yr in advance. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1920-1926.

Bohlin, T., Hamrin, S., Heggberget, T. G., Rasmussen, G. & Saltveit, S. J. 1989. Electrofishing - theory and practice with special emphasis on salmonids. *Hydrobiologia*, **173**, 9-43.

Bohlin, T., Sundstrom, L. F., Johnsson, J. I., Höjesjö, J. & Pettersson, J. 2002. Density-dependent growth in brown trout: effects of introducing wild and hatchery fish. *Journal of Animal Ecology*, **71**, 683-692.

Boon, A. K., Reale, D. & Boutin, S. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, **10**, 1094-1104.

Both, C., Dingemanse, N. J., Drent, P. J. & Tinbergen, J. M. 2005. Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology,* **74**, 667-674.

Brelin, D., Petersson, E., Dannewitz, J., Dahl, J. & Winberg, S. 2008. Frequency distribution of coping strategies in four populations of brown trout (*Salmo trutta*). *Hormones and Behavior*, **53**, 546-556.

Brick, O. 1998. Fighting behaviour, vigilance and predation risk in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, **56**, 309-317.

Brick, O. & Jakobsson, S. 2002. Individual variation in risk taking: the effect of a predatory threat on fighting behavior in *Nannacara anomala*. *Behavioral Ecology*, **13**, 439-442.

Bridcut, E. E. & Giller, P. S. 1995. Diet variability and foraging strategies in brown trout (*Salmo trutta*): an analysis from subpopulations to individuals. *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 2543-2552.

Brown, C. & Laland, K. 2001. Social learning and life skills training for hatchery reared fish. *Journal of Fish Biology*, **59**, 471-493.

Brown, C., Laland, K. & Krause, J. 2006. *Fish cognition and behaviour*. Oxford, UK: Blackwell Publishing Ltd.

Brown, M. E. 1946. The growth of brown trout (*Salmo trutta* Linn.) I. Factors influencing the growth of trout fry. *Journal of Experimental Biology*, **22**, 118-129.

Brydges, N. M., Colegrave, N., Heathcote, R. J. P. & Braithwaite, V. A. 2008. Habitat stability and predation pressure affect temperament behaviours in populations of three-spined sticklebacks. *Animal Behaviour*, **77**, 229-235.

Brännäs, E. & Johnsson, J. I. 2008. Behaviour and welfare in farmed fish. In: *Fish Behaviour* (Ed. by Magnhagen, C., Braithwaite, V. A., Forsgren, E. & Kapoor, B. G.), pp. 593-627. Enfield, USA: Science Publishers.

Bull, J. J. 1987. Evolution of phenotypic variance. *Evolution*, **41**, 303-315.

Bürger, R. & Gimelfarb, A. 2002. Fluctuating environments and the role of mutation in maintaining quantitative genetic variation. *Genetical Research*, **80**, 31-46.

Clarke, B. & O'Donald, P. 1964. Frequency-dependent selection. *Heredity*, **19**, 201-206.

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

Colgan, P. 1993. The motivational basis of fish behaviour. In: *Behaviour of teleost fishes* (Ed. by Pitcher, T. J.). London: Chapman & Hall.

Conrad, J. L. & Sih, A. 2009. Behavioural type in newly emerged steelhead *Oncorhynchus mykiss* does not predict growth rate in a conventional hatchery rearing environment. **75**, 1410-1426.

Couzin, I. D., James, R., Mawdsley, D., Croft, D. P. & Krause, J. 2006. Social organization and information transfer in schooling fishes. In: *Fish cognition and behaviour* (Ed. by Brown, C., Laland, K. & Krause, J.). Oxford: Blackwell Publishing.

Cutts, C. J., Metcalfe, N. B. & Taylor, A. C. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology*, **52**, 1026-1037.

Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734-739.

Darwin, C. R. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.*: John Murray.

Davies, N. B. 1976. Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). *Behaviour*, **59**, 280-294.

De Billy, V. D. & Usseglio-Polatera, P. 2002. Traits of brown trout prey in relation to habitat characteristics and benthic invertebrate communities. *Journal of Fish Biology*, **60**, 687-714.

Dellefors, C. & Faremo, U. 1988. Early sexual maturation in males of wild sea trout, *Salmo trutta* L, inhibits smoltification. *Journal of Fish Biology*, **33**, 741-749.

Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 398-408.

Dingemanse, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 847-852.

Dingemanse, N. J., Dochtermann, N. & Wright, J. 2010a. A method for exploring the structure of behavioural syndromes to allow formal comparison within and between data sets. *Animal Behaviour*, **79**, 439-450.

Dingemanse, N. J., Kazem, A. J. N., Réale, D. & Wright, J. 2010b. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, **25**, 81-89.

Dingemanse, N. J. & Reale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159-1184.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R. & Dawnay, N. 2007. Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, **76**, 1-11.

Dmitriew, C. & Rowe, L. 2007. Effects of early resource limitation and compensatory growth on lifetime fitness in the ladybird beetle (*Harmonia axyridis*). *Journal of Evolutionary Biology*, **20**, 1298-1310.

Dochtermann, N. A. 2010. Behavioral syndromes: carryover effects, false discovery rates, and *a priori* hypotheses. *Behavioral Ecology*, **21**, arq021.

Dochtermann, N. A. & Jenkins, S. H. 2007. Behavioural syndromes in Merriam's kangaroo rats (*Dipodomys merriami*): a test of competing hypotheses. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 2343-2349.

Duckworth, R. A. 2009. The role of behavior in evolution: a search for mechanism. *Evolutionary Ecology*, **23**, 513-531.

Dugatkin, L. A. 1997. Winner and loser effects and the structure of dominance hierarchies. *Behavioral Ecology*, **8**, 583-587.

Dugatkin, L. A. & Godin, J. G. J. 1992. Prey Approaching Predators - a Cost-Benefit Perspective. *Annales Zoologici Fennici*, **29**, 233-252.

Dukas, R. 2002. Behavioural and ecological consequences of limited attention. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **357**, 1539-1547.

Dukas, R. 1999. Costs of memory: ideas and predictions. *Journal of Theoretical Biology*, **197**, 41-50.

Dynesius, M. & Nilsson, C. 1994. Fragmentation and flow regulation of river systems in the northern 3rd of the world. *Science*, **266**, 753-762.

Einum, S. & Fleming, I. A. 2001. Implications of stocking: ecological interactions between wild and released salmonids. *Nordic Journal of Freshwater Research*, **75**, 56-70.

Elliott, J. M. 1994. *Quantitative ecology and the brown trout.* Oxford, UK: Oxford University Press.

Erman, A. 1896. Gespräch eines lebensmüden mit seiner seele. Aus dem papyrus 3024 der königlichen museen herausgegeben (mit 10 tafeln). *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, **2**, 1-77.

Falconer, D. S. & Mackay, T. F. C. 1996. *Introduction to Quantitative Genetics*, 4 edn. Essex, UK: Longman Green.

Ferguson, A. & Mason, F. M. 1981. Allozyme evidence for reproductively isolated sympatric populations of brown trout *Salmo trutta* L. in Lough Melvin, Ireland. *Journal of Fish Biology*, **18**, 629-642.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. & Skalski, G. T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist*, **158**, 124-135.

Fraser, D. J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evolutionary Applications*, **1**, 535-586.

Gallup, G. G. 1968. Mirror-image stimulation. *Psychological Bulletin*, **70**, 782-793.

Galsworthy, M. J., Paya-Cano, J. L., Liu, L., Monleon, S., Gregoryan, G., Fernandes, C., Schalkwyk, L. C. & Plomin, R. 2005. Assessing reliability, heritability and general cognitive ability in a battery of cognitive tasks for laboratory mice. *Behavior Genetics*, **35**, 675-692.

Garland, T. & Losos, J. B. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological morphology: integrative organismal biology* (Ed. by Wainwright, P. C. & Reilly, S. M.). Chicago: University of Chicago Press.

Godin, J. G. J. & Smith, S. A. 1988. A fitness cost of foraging in the guppy. *Nature*, **333**, 69-71.

Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45-86.

Gotceitas, V. & Godin, J.-G. J. 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.) : effects of social status and hunger. *Behavioral Ecology and Sociobiology*, **29**, 255-261.

Grant, J. W. A. 1993. Whether or not to defend - the influence of resource distribution. *Marine Behaviour and Physiology*, **23**, 137-153.

Grant, J. W. A. & Noakes, D. L. G. 1988. Aggressiveness and foraging mode of young-of-the-year brook charr, *Salvelinus fontinalis* (Pisces, Salmonidae). *Behavioral Ecology and Sociobiology*, **22**, 435-445.

Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C. & Kruuk, L. E. 2010. The misuse of BLUP in ecology and evolution. **175**, 116-125.

Hayes, J. P. & Jenkins, S. H. 1997. Individual variation in mammals. *Journal of Mammalogy*, **78**, 274-293.

Henderson, C. R. 1975. Best linear unbiased estimation and prediction under a selection model. *Biometrics*, **31**, 423-447.

Hofmann, H. A., Benson, M. E. & Fernald, R. D. 1999. Social status regulates growth rate: consequences for life-history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 14171-14176.

Houston, A., Clark, C., McNamara, J. & Mangel, M. 1988. Dynamic models in behavioral and evolutionary ecology. *Nature*, **332**, 29-34.

Huntingford, F. & Adams, C. 2005. Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*, **142**, 1207-1221.

Huntingford, F. A. 1976. The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, **24**, 245-260.

Huntingford, F. A. & Turner, A. K. 1987. *Animal Conflict*: Chapman and Hall.

Höjesjö, J., Johnsson, J. & Bohlin, T. 2004. Habitat complexity reduces the growth of aggressive and dominant brown trout (*Salmo trutta*) relative to subordinates. *Behavioral Ecology and Sociobiology*, **56**, 286-289.

Höjesjö, J., Johnsson, J. I. & Bohlin, T. 2002. Can laboratory studies on dominance predict fitness of young brown trout in the wild? *Behavioral Ecology and Sociobiology*, **52**, 102-108.

ICES. 2009. Report of the Baltic salmon and trout assessment working group (WGBAST).

Irschick, D. J., Meyers, J. J., Husak, J. F. & Le Galliard, J. F. 2008. How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research*, **10**, 177-196.

Jakobsson, S., Brick, O. & Kullberg, C. 1995. Escalated fighting behavior incurs increased predation risk. *Animal Behaviour*, **49**, 235-239.

Johnson, J. C. & Sih, A. 2005. Precopulatory sexual cannibalism in fishing spiders (*Dolomedes triton*): a role for behavioral syndromes. *Behavioral Ecology and Sociobiology*, **58**, 390-396.

Johnsson, J., Petersson, E., Jonsson, E., Bjornsson, B. T. & Jarvi, T. 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 1546-1554.

Johnsson, J., Winberg, S. & Sloman, K. A. 2006. Social interactions. In: *Behaviour and Physiology of Fish* (Ed. by Sloman, K. A., Wilson, R. W. & Balshine, S.), pp. 151-196: Elsevier.

Johnsson, J. I. 1993. Big and brave - size selection affects foraging under risk of predation in juvenile rainbow trout, *Oncorhynchus mykiss*. *Animal Behaviour*, **45**, 1219-1225.

Johnsson, J. I. & Bohlin, T. 2006. The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of The Royal Society B-Biological Sciences*, **273**, 1281-1286.

Johnsson, J. I., Clarke, W. C. & Withler, R. E. 1993. Hybridization with domesticated rainbow trout *(Oncorhynchus mykiss)* reduces seasonal variation in growth of steelhead trout (*O. mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 480-487.

Johnsson, J. I. & Kjällman-Eriksson, K. 2008. Cryptic prey colouration increases search time in brown trout (*Salmo trutta*): effects of learning and body size. *Behavioral Ecology and Sociobiology*, **62**, 1613-1620.

Johnsson, J. I. & Sundström, L. F. 2007. Social transfer of predation risk information reduces food locating ability in european minnows (*Phoxinus phoxinus*). *Ethology*, **113**, 166-173.

Kendal, R. L., Coolen, I., van Bergen, Y. & Laland, K. N. 2005. Trade-offs in the adaptive use of social and asocial learning. In: *Advances in the Study of Behavior, Vol 35*, pp. 333-379. San Diego: Elsevier Academic Press Inc.

Kingsolver, J. G., Hoekstra, H. E., Hoekstra, J. M., Berrigan, D., Vignieri, S. N., Hill, C. E., Hoang, A., Gibert, P. & Beerli, P. 2001. The strength of phenotypic selection in natural populations. *American Naturalist*, **157**, 245-261.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999. Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience & Biobehavioral Reviews*, **23**, 925-935.

Lack, D. 1943. The problem of partial migration. *British Birds*, **37**.

Lahti, K., Laurila, A., Enberg, K. & Piironen, J. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. *Animal Behaviour*, **62**, 935.

Lande, R. & Arnold, S. J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**, 1210-1226.

Lessells, C. M. & Boag, P. T. 1987. Unrepeatable repeatabilities - a common mistake. *Auk*, **104**, 116-121.

Lima, S. L. & Dill, L. M. 1990. Behavioral decisions made under the risk of predation - a review and prospectus. *Canadian Journal of Zoology*, **68**, 619-640.

Lind, J. & Cresswell, W. 2005. Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, **16**, 945-956.

Logue, D. M., Mishra, S., McCaffrey, D., Ball, D. & Cade, W. H. 2009. A behavioral syndrome linking courtship behavior toward males and females predicts reproductive success from a single mating in the hissing cockroach, *Gromphadorhina portentosa*. *Behavioral Ecology,* **20**, 781-788.

Lythgoe, J. N. 1979. *The ecology of vision*. Oxford: Oxford University Press.

Magnhagen, C. & Staffan, F. 2005. Is boldness affected by group composition in young-of-the-year perch (*Perca fluviatilis*)? *Behavioral Ecology and Sociobiology*, **57**, 295-303.

Magurran, A. E. 1993. Individual differences and alternative behaviours. In: *Behaviour of teleost fishes* (Ed. by Pitcher, T. J.). London: Chapman & Hall.

Magurran, A. E. 1986. Predator inspection behavior in minnow shoals - differences between populations and individuals. *Behavioral Ecology and Sociobiology*, **19**, 267-273.

Mangel, M. & Stamps, J. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research*, **3**, 583-593.

Martin, P. & Bateson, P. 1990. *Measuring behaviour: and introductory guide*. Cambridge: Cambridge university press.

Martins, T. L. F., Roberts, M. L., Giblin, I., Huxham, R. & Evans, M. R. 2007. Speed of exploration and risk-taking behavior are linked to corticosterone titres in zebra finches. *Hormones and Behavior*, **52**, 445.

Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.

McElreath, R. & Strimling, P. 2006. How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Animal Behaviour*, **72**, 1135-1139.

McNamara, J. M. & Houston, A. I. 1986. The common currency for behavioral decisions. *American Naturalist*, **127**, 358-378.

McNeil, W. J. 1991. Expansion of cultured Pacific salmon into marine ecosystems. *Aquaculture*, **98**, 173-183.

Meekan, M. G., von Kuerthy, C., McCormick, M. I. & Radford, B. 2010. Behavioural mediation of the costs and benefits of fast growth in a marine fish. *Animal Behaviour*, **79**, 803-809.

Metcalfe, N. B. 1986. Intraspecific variation in competitive ability and food intake in salmonids - consequences for energy budgets and growth rates. *Journal of Fish Biology*, **28**, 525-531.

Milinski, M. & Heller, R. 1978. Influence of a predator on optimal foraging behavior of sticklebacks (*Gasterosteus aculeatus* L.). *Nature*, **275**, 642-644.

Millidine, K. J., Armstrong, J. D. & Metcalfe, N. B. 2009. Juvenile salmon with high standard metabolic rates have higher energy costs but can process meals faster. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 2103-2108.

Monclús, R., Rödel, H. G., Von Holst, D. & De Miguel, J. 2005. Behavioural and physiological responses of naïve European rabbits to predator odour. *Animal Behaviour*, **70**, 753-761.

Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, **100**, 403-405.

O'Connell, M. & Wright, J. M. 1997. Microsatellite DNA in fishes. *Reviews in Fish Biology and Fisheries*, **7**, 331-363.

Olla, B. L., Davis, M. W. & Ryer, C. H. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. *Bulletin of Marine Science*, **62**, 531-550.

Overli, O., Sorensen, C., Pulman, K. G. T., Pottinger, T. G., Korzan, W., Summers, C. H. & Nilsson, G. E. 2007. Evolutionary background for stress-coping styles: relationships between physiological, behavioral, and cognitive traits in non-mammalian vertebrates. *Neuroscience & Biobehavioral Reviews*, **31**, 396.

Pearce, J. M. 1997. *Animal learning and cognition: an introduction*, 2 edn. London: Psychology press.

Pettersson, J., Johnsson, J. I. & Bohlin, T. 1996. The competitive advantage of large body size declines with increasing group size in rainbow trout. *Journal of Fish Biology*, **49**, 370-372.

Pigliucci, M. 2001. *Phenotypic plasticity. Beyond Nature and Nurture.*: The Johns Hopkins University Press.

Pinheiro, J. C. & Bates, D. B. 2000. *Mixed effects models in S and S-Plus*. New York: Springer Verlag.

Pintor, L. M., Sih, A. & Bauer, M. L. 2008. Differences in aggression, activity and boldness between native and introduced populations of an invasive crayfish. *Oikos*, **117**, 1629-1636.

Promislow, D. E. L. & Harvey, P. H. 1990. Living fast and dying young - a comparative analysis of life-history variation among mammals. *Journal of Zoology*, **220**, 417-437.

Quinn, G. P. & Keough, M. J. 2002. *Experimental design and data analysis for biologists*. Cambridge: Cambridge university press.

Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A. & Sheldon, B. C. 2009. Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology*, **78**, 1203-1215.

Ragland, G. J. & Carter, P. A. 2004. Genetic covariance structure of growth in the salamander *Ambystoma macrodactylum*. *Heredity*, **92**, 569-578.

Réale, D. & Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, **65**, 463-470.

Reale, D., Martin, J., Coltman, D. W., Poissant, J. & Festa-Bianchet, M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, **22**, 1599-1607.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T. & Dingemanse, N. J. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews*, **82**, 291-318.

Reisenbichler, R. R. & Rubin, S. P. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. *ICES Journal of Marine Science*, **56**, 459-466.

Reznick, D., Bryant, M. J. & Bashey, F. 2002. r- and K-selection revisited: the role of population regulation in life-history evolution. *Ecology*, **83**, 1509-1520.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223-225.

Ricklefs, R. E. & Scheuerlein, A. 2003. Life span in the light of avian life histories. *Population and Development Review*, **29**, 71-98.

Ricklefs, R. E. & Wikelski, M. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution*, **17**, 462-468.

Riddell, B. E. & Swain, D. P. 1991. Competition between hatchery and wild coho salmon (*Oncorhynchus kisutch*): genetic variation for agonistic behaviour in newly-emerged wild fry. *Aquaculture*, **98**, 161-172.

Riechert, S. E. & Hedrick, A. V. 1993. A test for correlations among fitness-linked behavioural traits in the spider *Agelenopsis aperta* (Araneae, Agelenidae). *Animal Behaviour*, **46**, 669-675.

Rincon, P. A. & Lobon-Cervia, J. 1999. Prey-size selection by brown trout (*Salmo trutta* L.) in a stream in northern Spain. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **77**, 755-765.

Ringler, N. H. 1985. Individual and temporal variation in prey switching by brown trout, *Salmo trutta*. *Copeia*, 918-926.

Roussel, J. M., Haro, A. & Cunjak, R. A. 2000. Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 1326-1329.

Ruxton, G. D. & Colegrave, N. 2006. *Experimental design for the life sciences*, 2 edn. Oxford: Oxford university press.

Ruzzante, D. E. & Doyle, R. W. 1991. Rapid behavioral changes in medaka (*Oryzias latipes*) caused by selection for competitive and noncompetitive growth. *Evolution*, **45**, 1936-1946.

Satterlee, D. G. & Jones, R. B. 1997. Ease of capture in Japanese quail of two lines divergently selected for adrenocortical response to immobilization. *Poultry Science*, **76**, 469-471.

Shumway, C. A. 1999. A neglected science: applying behavior to aquatic conservation. *Environmental Biology of Fishes*, **55**, 183-201.

Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? , **210**, 1041-1043.

Sih, A. & Bell, A. 2008. Insights from behavioral syndromes for behavioral ecology. In: *Advances in the Study of Behavior*.

Sih, A., Bell, A. & Johnson, J. C. 2004a. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372-378.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004b. Behavioral syndromes: an integrative overview. *Quarterly Review of Biology*, **79**, 241-277.

Sloman, K. A. & Armstrong, J. D. 2002. Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? *Journal of Fish Biology*, **61**, 1-23.

Sluyter, F., Bult, A., Lynch, C. B., Vanoortmerssen, G. A. & Koolhaas, J. M. 1995. A comparison between house mouse lines selected for attack latency or nest-building: evidence for a genetic basis of alternative behavioral strategies. *Behavior Genetics*, **25**, 247-252.

Sneddon, L. U., Hawkesworth, S., Braithwaite, V. A. & Yerbury, J. 2006. Impact of environmental disturbance on the stability and benefits of individual status within dominance hierarchies. *Ethology*, **112**, 437-447.

Stamps, J. A. 2007. Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, **10**, 355-363.

Stearns, S., Dejong, G. & Newman, B. 1991. The effects of phenotypic plasticity on genetic correlations. *Trends in Ecology & Evolution*, **6**, 122-126.

Stoks, R., De Block, M., Van de Meutter, F. & Johansson, F. 2005. Predation cost of rapid growth: behavioural coupling and physiological decoupling. *Journal of Animal Ecology*, **74**, 708-715.

Strandberg, E., Jacobsson, J. & Saetre, P. 2005. Direct genetic, maternal and litter effects on behaviour in German shepherd dogs in Sweden. *Livestock Production Science*, **93**, 33-42.

Sundbaum, K. & Näslund, I. 1998. Effects of woody debris on the growth and behaviour of brown trout in experimental stream channels. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **76**, 56-61.

Sundström, L. F. & Johnsson, J. I. 2001. Experience and social environment influence the ability of young brown trout to forage on live novel prey. *Animal Behaviour*, **61**, 249-255.

Sundström, L. F., Petersson, E., Höjesjö, J., Johnsson, J. I. & Jarvi, T. 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioral Ecology*, **15**, 192-198.

Waddington, C. H. 1942. Canalization of development and the inheritance of acquired characters. *Nature*, **150**, 563-565.

van Bergen, Y., Coolen, I. & Laland, K. N. 2004. Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 957-962.

van Oers, K., de Jong, G., Drent, P. J. & van Noordwijk, A. J. 2004. A genetic analysis of avian personality traits: correlated, response to artificial selection. *Behavior Genetics*, **34**, 611-619.

van Oers, K., de Jong, G., van Noordwijk, A. J., Kempenaers, B. & Drent, P. J. 2005. Contribution of genetics to the study of animal personalities: a review of case studies. *Behaviour*, **142**, 1185-1206.

Vanhooydonck, B., Damme, R. V. & Aerts, P. 2001. Speed and stamina trade-off in lacertid lizards. *Evolution*, **55**, 1040.

Wedekind, C. 2002. Sexual selection and life-history decisions: implications for supportive breeding and the management of captive populations. *Conservation Biology*, **16**, 1204-1211.

Verhoeven, K. J. F., Simonsen, K. L. & McIntyre, L. M. 2005. Implementing false discovery rate control: increasing your power. *Oikos*, **108**, 643-647.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annual Review of Ecology and Systematics*, **20**, 249-278.

Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991. Producers, Scroungers, and Group Foraging. *The American Naturalist*, **137**, 847-863.

Wilson, A. D. M., Godin, J. G. J. & Ward, A. J. W. 2010a. Boldness and reproductive fitness correlates in the eastern mosquitofish, *Gambusia holbrooki*. *Ethology*, **116**, 96-104.

Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., Kruuk, L. E. B. & Nussey, D. H. 2010b. An ecologist's guide to the animal model. *Journal of Animal Ecology*, **79**, 13-26.

Wilson, D. S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of The Royal Society of London Series B-Biological Sciences*, **353**, 199-205.

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

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

Wolf, M., van Doorn, G. S., Leimar, O. & Weissing, F. J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581-584.

Wolf, M., van Doorn, G. S. & Weissing, F. J. 2008. Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, **105**, 15825-15830.

Vollestad, L. A. & Quinn, T. P. 2003. Trade-off between growth rate and aggression in juvenile coho salmon, *Oncorhynchus kisutch*. *Animal Behaviour*, **66**, 561-568.