

**ONTOGENETIC AND MORPHOLOGICAL
EFFECTS OF PERSONALITY IN COMMON
CARP (*CYPRINUS CARPIO*)**

A Thesis Submitted to the College of Graduate Studies and Research in Partial Fulfillment of
the Requirements for the Degree of Master of Science in the Department of Biology
University of Saskatchewan

By

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ABSTRACT

The field of animal personality has been growing rapidly in the past 10 years, yet relatively little attention has been given to development of personality through ontogeny. To understand the stability of personality traits throughout animal's life is particularly important as behavioural tendencies are likely to change in response to the different trade-offs animals face at each stage of the life cycle. The purpose of this research was to examine the stability of personality traits in common carp but also to determine whether personality traits can affect production of induced morphological defences in this species.

To investigate the presence of behavioural syndrome and the stability of individual behaviours through ontogeny, common carp were monitored for a period of 10 months. Two different tests were used to investigate cross-situational consistency in behavioural traits: exploration and risk-taking. Juvenile carp were monitored at different time intervals to assess behavioural stability. Finally, morphometric data were collected to examine the link between body morphology and behavioural traits.

No initial cross-situational consistency in behaviours was observed in juvenile common carp. Ranking of behaviour traits was consistent over a period of 14-16 weeks but not when the time interval was longer. Young carp that ranked lowest in both shelter use and activity used shelter significantly more compared to those individuals that ranked highest in use of shelter and activity even after a 10 month period. Development of a deeper body was also associated with the extreme levels of shelter seeking and activity. Fish pre-determined as being "Active" increased their body depth significantly more than did "Passive" fish. To my knowledge, this is the first study directly linking personality traits and change in body morphology in an aquatic species.

ACKNOWLEDGEMENTS

I would like to thank my supervisor Professor Douglas Chivers and my co-supervisor Dr. Maud Ferrari for their guidance and support throughout the last three years.

I would also like to thank my advisory committee consisting of Dr. Joseph Stookey, Dr. Robert Clark and Dr. Gary Bortolotti for their support and helpful suggestions throughout my research.

Many people have been involved in this long term project. My biggest thanks go to my lab member and dear friend Zach Hoover who helped me day and night with setting up my flow-through system. I would also like to thank other lab members namely Adi Manek and Iain Philips and my undergraduate volunteers Bryony Griffiths, Kelsey Allen and Robyn Campbell who were a great help throughout the whole project.

I would like to thank the friendly staff at the Department of Biology for their assistance with pretty much any problem I had.

Finally, I would like to thank my family and friends all over the world for always being there for me and listening.

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CHAPTER ONE: INTRODUCTION

1.1: Background and terminology

In ever-changing environments, animals need to constantly assess imminent and long term risks and modify their behaviours accordingly. To forage (or not) under the risk of predation is just one of the examples of decision-making processes animals have to undergo on a day to day basis (Lima & Dill 1990). As a consequence, many species across diverse taxa developed mechanisms by which they reduce their predation pressure (Brönmark & Miner 1992; Trussell & Smith 2000; Kishida & Nishimura 2004). These include behavioural (Mathis et al. 2003; Foam et al. 2005), morphological (Brönmark & Miner 1992; Eklöv & Jonsson 2007; Abate et al. 2010) and life history changes (Chivers et al. 2001; Kusch & Chivers 2004). Of these, behavioural adaptations are the only mechanisms that can provide rapid (even instant) response to predation threat. Thus animal behaviour was considered to be a plastic trait enabling individuals to adapt to variable environmental conditions. As a result, studies attributed individual differences in behaviour to be “noise” around an adaptive mean (Réale et al., 2007; Schuett et al. 2010). Yet scientists are discovering that animals often show individual behavioural differences with limited plasticity and these differences are observed across several taxa including fish (three-spined stickleback (*Gasterosteus aculeatus*), Bell & Sih 2007; guppy (*Poecilia reticulata*), Dyer et al. 2009; common carp, Huntingford et al. 2010; brook charr (*Salvelinus fontinalis*), Wilson & McLaughlin 2007; for more fish species see Conrad et al. 2011). These behavioural differences among individuals are consistent over time and across different contexts, and are referred to as: personality, behavioural syndrome, behavioural profile, and copying style or temperament (Sih et al. 2004b; Réale et al. 2007; Schuett et al. 2010). Limited behavioural plasticity means that animals may not adequately modify their behaviour in response to environmental change and can face a trade-off. For example, individuals that are bolder, or more active, possess an advantage over shy conspecifics in environments that lack predators. Their risk-taking enables them to obtain resources more readily. However, in the presence of a predator, higher risk-taking can increase the chances of encountering a predator and in this case risk-averse, shyer individuals have an advantage (Bell & Sih 2007; Sih et al. 2012).

The terminology associated with personality research can be confusing. Despite the fact that some scientists do not consider these terms to be interchangeable (Sih et al., 2004; Stamps and Groothuis, 2010), the terms “personality” or “behavioural syndrome” tend to be used frequently and interchangeably in behavioural ecology. Behavioural syndrome is defined as: ” A suite of correlated behaviours reflecting between-individual consistency in behaviour across multiple (two or more) situations” (Sih et al. 2004b). It is important to note that the word “consistent” does not imply that the actual behavioural trait values cannot change with age or environmental conditions, it is the differences between individuals in selected population that are considered to be maintained (i.e., their rank order is maintained, Sih et al., 2004; Réale et al., 2007). Therefore, while an animal might change the level of a behaviour, such as aggression, in response to environmental factor (e.g. predation, mating), some individuals in the population will be more aggressive in general across different contexts (Sih et al. 2004, but see section 1.3 Development of personality).

In a framework proposed by Réale et al. (2007) personality traits were divided into five broad categories: shyness-boldness, exploration-avoidance, activity, aggressiveness and sociability (Table 1). To quantify personality traits, each individual needs to be observed at least twice in different contexts (Sih et al. 2004b; Bell 2007). Standard behavioural observations have been developed to test each of the behavioural traits (Table 1, examples of tests used in aquatic ecology) and in most cases correlated traits are combined into one personality score. Individuals then fall anywhere along a certain axis, such as the shy-bold continuum, with the shyest and the boldest being the two ends of the continuum (Réale et al. 2007). In general, bold individuals are characterized by their willingness to take a higher degree of risk and therefore, are more likely to approach novel objects or food (Kурvers et al. 2009), exhibit a greater tendency to explore a novel environment (Dingemanse et al. 2004) and spend more time in open habitats (Wilson & McLaughlin 2007), whereas the opposite is true for shy individuals.

Table 1: The five personality categories as proposed by Réale et al. (2007). Listed are examples of behavioural tests commonly used in aquatic species.

Personality category	Description	Examples (aquatic research)
Shyness-boldness	Individual's reaction to risky, but not new, situation	Reaction to predatory attack (Bell & Sih 2007), handling
Exploration-avoidance	Individual's reaction to a new habitat	Reaction to novel food, environment (Huntingford et al. 2010), object (Dyer et al. 2009)
Activity	General level of activity in non-risky environment	Midline crosses, time spent moving (Wilson & Godin 2009)
Aggressiveness	Individual's agonistic reaction towards conspecifics	Number of bites or chases (Huntingford 1976b), mirror test (Adriaenssens & Johnsson 2013)
Sociability	Individual's reaction to the presence or absence of conspecifics	Shoaling cohesion (Dyer et al. 2009), neighbouring index, time spent shoaling (Ward et al. 2004)

The concept of animal personality is relatively new field in behavioural ecology. One of the first studies documenting the existence of personality in animals was published in 1976 by Huntingford using three-spined stickleback as experimental subject. She found consistent individual differences in aggression towards conspecifics and heterospecifics throughout the whole breeding season. The level of aggression also positively correlated with boldness towards predatory pike (Huntingford 1976a, 1976b). Huntingford's ground-breaking research instigated great interest in the field of animal personality which in the last 10 years or so has grown into a large area of behavioural ecology and comparative psychology.

1.2: Evolution of personality

The rather limited behavioural plasticity that personality traits are recognized for has been puzzling behavioural and evolutionary ecologists. How do personality traits evolve, and more importantly, why do these seemingly maladaptive traits persist in natural populations?

Behavioural flexibility should provide selective advantage, yet in the case of behavioural syndromes, animals are seemingly limited in their response which can be costly (Johnson & Sih 2005).

The trade-off hypothesis is one of the possible explanations to what maintains variation in risk-taking in natural populations (Sih et al. 2004a). For example, bold individuals may do well in one context resulting in higher fitness, while shy individuals may do well in another. Meta-analysis of published studies investigating the effects of single personality traits on fitness revealed that bolder individuals have higher reproductive success compared to shyer ones. On the other hand, bolder individuals had also a shorter life span meaning both behavioural types had the same overall fitness (Smith & Blumstein 2008). Thus, a range of behavioural types can coexist when environmental variation exists (Sih et al. 2004a).

Empirical studies on how personality traits are maintained in the wild can be very difficult, and require a long term monitoring of selected populations. A study of wild population of great tits (*Parus major*) is an excellent example of how selection maintains different personality traits in population living in fluctuating environment. Dingemanse et al. (2004) found that in poor winters, fast-exploring females and slow-exploring males had higher survival success. They suggest that fast-exploring females have an advantage over slow-exploring females in poor years due to their higher success to locate clumped resources. On the other hand, the lower aggressiveness of slow-exploring females results in lower mortality in rich years. In addition, fast-exploring territorial males may benefit in rich years, when competition for space is high and therefore their increased aggressiveness may improve their chances in excluding competitors. However in poor years, overt aggressiveness may not be beneficial and may reduce the survival of fast-exploring territorial males (Dingemanse et al. 2004).

Several models have been proposed to explain evolution of behavioural syndromes and were reviewed in Dingemanse & Wolf (2010). Perhaps the most referenced model by Wolf et al. (2007) is based on trade-offs between current and future reproduction when the quality of resources in the environment are manipulated. Individuals that chose to explore environment thoroughly (hence obtain high-quality resources) invest a lot in future reproduction, while those that explore environment superficially put more emphasis on current reproduction. If other factors, such as aggression towards conspecifics or predation,

are included in the model, those individuals that have more to lose (in this case thorough explorers) should behave cautiously and those that have less to lose should take higher risks (Wolf et al. 2007). However, the dimorphism can only emerge when certain restrictions exist, such as the difficulty of rearing offspring and looking for high-quality habitat at the same time (Massol & Crochet 2008). Another criticism of this model came from McElreath et al. (2007) who argue that the asset protection (i.e., individuals that have more to lose take less risk) is a negative feedback process which over time makes individuals more alike, not less.

1.3: Development of personality through ontogeny

The questions that now arise are, "Why are some individuals consistently bolder, or more aggressive than others throughout their entire life?", "Can personality change over the life span of an individual as the strength of different environmental factors and their associated trade-offs changes?", and "Are personality traits really fixed, or can we see some level of plasticity?" The need for developmental approach to personality has been expressed by several researches (Bell & Stamps 2004; Conrad et al. 2011; Groothuis & Trillmich 2011; Trillmich & Hudson 2011; Wilson & Krause 2012b) as this topic has been relatively unexplored by behavioural ecologists until recently. Behavioural tendencies that are stable over short periods of time are likely to change over longer periods, especially when linked to underlying physiological processes such as growth (Stamps & Groothuis 2010). Biro and Stamps (2008) proposed framework suggesting that animal personality traits and life-history traits are closely linked. An example include species where boldness, aggressiveness and activity are all positively correlated with food intake and thus with growth rates and fecundity (Réale et al. 2000). Bolder individuals with higher resource acquisition then establish their life history trajectory as juveniles, and while deviating from it is possible, it is also costly (Biro & Stamps 2008).

Genetic constraints can also limit the range of behavioural plasticity. Correlational selection then acts on several behavioural traits rather than optimizing behaviours in each context (Johnson & Sih 2005). In the fishing spider (*Dolomedes triton*), juvenile and adult voracity were positively correlated. In addition, voracity towards hetero-specific prey was positively correlated with boldness towards predators and with precopulatory sexual cannibalism, a behaviour that is seemingly detrimental for individual's overall fitness. However, the benefits of juvenile voracity, such as juvenile feeding rate, the positive

correlation with fixed adult size and fecundity, outweigh any fertility costs associated with female sexual cannibalism (Johnson & Sih 2005).

One can easily see how personality traits that increase food intake and resource acquisition can be linked to life-history traits in a stable environment. In the next section (1.4) I give examples of several studies reporting the effect of personality on foraging success. But, when a strong selection pressure is introduced to what previously was a stable environment, new behavioural correlations may be created. In sticklebacks, a live predation event generated a boldness-aggressiveness behavioural correlation. This correlation did not exist before the predation event, and was produced by phenotype-dependent predations as well as by coupling behaviours that seem to be advantageous when predation selection is strong (Bell & Sih 2007). Similarly, emergence of behavioural syndrome after strong selection was observed in nature. Adriaenssens and Johnsson (2013) subjected young (2.5 month old), wild brown trout (*Salmo trutta*) to series of behavioural assays and subsequently released them back to the wild. After two months, fish were re-captured and tested again. While the younger fish did not show consistency across different behavioural assays, after 2 months in the wild their behaviour was much more predictable and highly exploratory individuals were also more aggressive (Bell 2012; Adriaenssens & Johnsson 2013).

Stability of behavioural syndrome over ontogeny does not necessarily imply stability of individual behaviours. For example, Bell and Stamps (2004) found aggression, boldness and activity alone to be unstable over time in population of three-spined stickleback. Yet a positive correlation between aggression and boldness was stable over ontogeny, meaning the behavioural syndrome, but not the individual behaviours were stable. From individual point of view, a young fish that is very aggressive and bold can be timid and shy as an adult. Similar stability in behavioural syndrome but plasticity in individual behaviours was observed in hatchery-reared brown rockfish, *Sebastes auriculatus* (Lee & Berejikian 2008). These studies suggest that behavioural plasticity can occur in response to different environmental conditions later in life. Yet there is a possible constraint to this plasticity, such as change in one behaviour cannot occur without changes in other behaviour belonging to the same syndrome (Bell & Stamps 2004).

For species with abrupt life cycle changes, de-coupling of behavioural syndromes would be expected to occur due to the complete change in environmental conditions. In amphibians, undergoing metamorphosis results in ecological niche shift with dramatic changes in predation pressure and foraging strategies between the juvenile tadpole stage and the adult frog stage. To date, the only study looking at consistency of personality traits across

metamorphosis in vertebrates was performed by Wilson & Krause (2012a). They found consistency in personality traits within given life cycle stages (tadpole, or frog) in common lake frog (*Rana ridibunda*), but more importantly, activity and exploration traits were consistent over metamorphosis (Wilson & Krause 2012a).

The shortage of studies investigating the development of personality traits may stem from the consistency concept that is such an essential part of the definition of personality (Groothuis & Trillmich 2011). Yet the above experiments demonstrated that plasticity in behavioural traits may exist but may not occur independently if coupled with other behaviours in a syndrome. Another reason may be the difficulty of following a wild animal through several stages in ontogeny. While this can be partially overcome by studying individuals in laboratory, the drawback is the possibility of producing artificial results that may not reflect the relationships in the wild (Adriaenssens & Johnsson 2011). In addition, designing behavioural tests that will measure the same personality traits but at different life stages can be tricky, but are vital in order to understand whether the observed relationship is true change in personality or just a set of different behaviours describing the same personality trait (Groothuis & Trillmich 2011).

1.4: Personality and foraging success

Individual differences in risk-taking, exploration and activity are most likely to be related to foraging success. A multitude of scientific papers documents the link between personality and foraging success both in the laboratory and the wild. For example, in birds, individuals that were exploratory in captivity were also more likely to find newly introduced feeding stations in the wild, and the opposite was true for birds with reduced exploratory tendency (Herborn et al. 2010). Another study shows positive correlation between personality and dominance status, resulting in bold and dominant individuals spending more time feeding due to their competitive advantage (David et al. 2011). In a more relevant fish example, the relationship between boldness and dominance was also found in the three-spined sticklebacks (Ward *et al.*, 2004). Bold individuals not only out-competed shy individuals for food but they were also more likely to occupy frontal, beneficial positions in a shoal. Their increased competitive ability and the positioning in a group were reflected in their increased growth rate compared to the shy individuals (Ward *et al.*, 2004). Increased willingness to approach a novel feeder was also found in fish shoals consisting of either all bold individuals, or in

mixed shoals (50% bold and 50% shy), but shoals with all shy individuals approached the novel feeding device significantly slower (Dyer *et al.* 2009).

One of the frameworks explaining the evolution of personality is their link to life-history traits. Difference in resource acquisition then leads to increased growth and fecundity (Biro & Stamps 2008). The above empirical research supports this theory. Personality can increase foraging success either through willingness to explore new areas and foods, or through excluding competitors in species where dominance and boldness are positively correlated.

1.5: Carp and morphological adaptations

Morphological adaptations are one of the induced defences animal can develop in response to predation pressure. In an aquatic environment, the development of spines (Reist 1980) or deeper bodies (Eklöv & Jonsson 2007; Abate *et al.* 2010) act as defence against piscivorous predators. Crucian carp (*Carassius carassius*) has been widely studied aquatic example of predator-induced defences. In the presence of piscivorous predator, such as northern pike (*Esox lucius*), crucian carp increases its body depth (Brönmark & Miner 1992; Brönmark & Pettersson 1994; Nilsson *et al.* 1995; Andersson *et al.* 2006, Figure 1). Reduced food resources can influence the ability to exhibit this induced trait (Chivers *et al.* 2008). Yet, as would be expected, this morphological adaptation has associated trade-offs. Deep-bodied morphs suffer a substantial cost when competing with shallow-bodied conspecifics (Pettersson & Brönmark 1997) and have higher energy expenditure when swimming (Pettersson & Brönmark 1999).



Figure 1: Shallow (a) and deep-bodied (b) form of the crucian carp (*Carassius carassius*). Scale bars, 10 mm (Domenici *et al.* 2008)

The general understanding was that the production of morphological defences is a direct response to the presence of predators. Although a recent review published by Bourdeau and Johansson (2012) suggests that predator induced morphological defences may be a by-product of alteration in behaviour in response to predation. In many aquatic species the

typical fright response to the presence of predator is to decrease activity levels (Ferrari et al. 2010) which is also true for crucian carp (Holopainen et al. 1997; Johansson & Andersson 2009). The reduction in activity conserves energy, which can be relocated to growth and thus change in morphology occurs (Holopainen et al. 1997; Bourdeau & Johansson 2012). Support of this relationship can be found in the extensive crucian carp research. Johansson and Andersson (2009) showed that both predation risk and standing water current independently induced deeper body shape in crucian carp. Another variable that can induce a deeper body shape is diet. Crucian carp fed benthic prey developed deeper bodies in relation to carp raised on zooplankton diet. Increased body depth allows for higher precision and manoeuvrability when feeding on sedentary organisms (Andersson et al. 2006; Domenici et al. 2008).

To summarize, evidence clearly suggests that change in body depth can be induced by the presence of a piscivorous predator. Yet, as I highlighted above, other mechanisms such as reduced activity and diet can produce similar change in body depth without the presence of predation threat.

1.6: Objectives of this study

The overall objectives of my thesis are twofold. First, to study personality traits and their temporal consistency in juvenile common carp over a one year period. In a review by Conrad et al. (2011), boldness and exploration show positive correlation in most studies involving fish. Thus, I predicted a similar positive relationship to be observed in common carp. In a majority of personality studies, tests are repeated over a short period of time, such as a few days or weeks. I had a chance to record behaviours of young common carp throughout a relatively long period of intensive growth and development (i.e., months), thus contributing new information to the field of personality development through ontogeny.

The second objective of this study is to investigate the effect of personality on foraging success in common carp. This species was chosen because it is a close relative to crucian carp and goldfish, both known to be able to produce deep-body morphology. However, change in body depth in response to environmental variability has never been shown in common carp which provides a great opportunity to study the link between morphology and personality in this species. I have already discussed how both activity and willingness to approach novel food or feeders can consistently differ between individuals. In

addition, both food and activity can affect body depth in some fish species. Therefore, I propose that consistent individual variation in personality may indirectly affect individual's ability to develop deeper body in this species. To my knowledge this is the first study investigating the link between personality and morphology in aquatic vertebrates.

CHAPTER TWO: MATERIALS AND METHODS

Common carp eggs were obtained from OSAGE catfisheries, Inc. (Osage Beach, Missouri) and raised in the laboratory. After hatching, juvenile carp were kept in 74 L flow-through stock tanks (density 30 - 40 fish/ tank) until the beginning of the experiment. Each stock tank was screened off from visual disturbance. Fish were fed adequate food depending on their age (fry: brine shrimp larvae; younger fish: bloodworms, commercial tropical fish flakes Rolf C. Hagen Inc., QC, Canada; older fish: floating pellets Top Fin® Pond Fish Food). Fry and younger fish were fed twice a day to satiation. At the start of the experiment fish were 13 months old (weight range: 0.51 g - 34.69 g) and were fed once a day to satiation. Any changes in feeding related to experimental procedure are discussed below. The experiment was carried out from May 2012 - March 2013. By the end of the experiment fish were 23 months old (weight range: 7.23 g - 87.26 g; for the entire timeline of the Master's thesis see Figure 2.2). In all tests sex was not taken into account because carp do not reach sexual maturity until about 3 - 4 years of age, weighing around 1500 g (Jhingran & Pullin 1985). The temperature throughout the whole experiment was kept constant at 17 ± 1 °C, and photoperiod was maintained at 16L:8D hr. Water quality parameters were checked weekly to ensure that the health of fish was not compromised.

Prior to personality testing, each individual was tagged using Visible Implant Elastomer tags (VIE, Northwest Marine Technology, Inc; Figure 2). Different colour and position combinations injected into the dorsal epidermis gave a unique identification code to each fish (Croft et al. 2003). Ultraviolet light increased the visibility of the tag allowing for identification of fish several months after the tagging. Personality testing was commenced about one month after tagging to reduce bias associated with handling stress.



Figure 2: Positioning of VIE (Visible Implant Elastomer) tag near the dorsal fin of a common carp

2.1: Determination of behavioural type- Individual personality

Each fish was tested for behavioural type by combining two behavioural observations to determine whether individual behaviours are consistent over different contexts: (1) exploration of a novel environment and (2) response to danger stimuli. These two tests are widely used in fish personality studies and in most cases show positive correlation (Conrad et al. 2011). The behavioural traits clearly fall into two separate categories proposed by Réale et al. (2007; see introduction). All individuals were subjected to the same sequence of personality tests starting with the novel environment (NE) test immediately followed by the simulated predator attack (SPA) test. Temperature of the experimental tanks was matched to that of the holding tanks. At least 12 hr before the start of the behavioural trials fish were fed to satiation in their stock tanks. One hour feeding period was allowed after which leftover food was siphoned out. To minimize disturbance to the fish, three walls of the experimental tanks were covered. Behavioural observations were made through a small opening adjacent to the tank.

2.1.1.: The novel environment test

The exploration-avoidance trait is described as individual's reaction to a new situation, such as novel habitat, food or object (Réale et al. 2007). The experimental methods for the novel environment test were a slight modification of the methods used by Huntingford et al. (2010) who had previously performed this test in common carp. Screening tanks (74 L; Figure 2.1.1) consisted of an acclimatization compartment (21 cm x 31.5 cm x 41 cm) and a novel environment compartment (40 cm x 31.5 cm x 41 cm). A black plexiglass divider with remotely operated door was installed between the two compartments. The novel chamber contained gravel (1 cm in depth) and three plastic plants. At the start of the screening, an individual fish was placed into the acclimatization chamber for 15 minutes. At the end of the acclimatization period the removable door was raised and the time it took the fish to enter the novel chamber was measured. Fish that did not enter the novel environment were given



Figure 2.1.1: Observational tank for the novel environment test.

maximum time of 10 minutes (600 s). A five centimetre grid was drawn on the wall of the novel environment and the number of lines fish crossed, as well as the position of each square that the fish entered was noted (for detailed description of all behaviours observed see Table 2).

2.1.2: The simulated predator attack test

According to Réale et al. (2007) the shyness-boldness trait is described as individual's reaction to any risky situation, but not a new situation. This trait was observed in the simulated predator attack test. The experimental methods for this behavioural observation were slight modification of methods used by Ward et al. (2004). A special observation tank was made to test the response of carp to a simulated predator attack. A clear plexiglass divider was installed in the observation tank separating the tank into two sections: the main section where the fish was placed (35 cm x 31.5 cm x 20 cm) and a smaller section with gravel and plants. Horizontal and vertical midlines were drawn on the plexiglass divider as well as on the walls of the main compartment. The simulated predator attack was produced by remotely dropping a weight into the tank (Figure 2.1.2). The reason for the smaller compartment was to make sure fish orients towards this compartment and spends most of the time near the plexiglass divider. This is where the weight is dropped; hence increasing the likelihood that fish will fully experience the simulated attack. Several plastic plants were positioned at the back of the main compartment to act as a shelter. Individual fish was placed into the main compartment and left to acclimatize for 15 min. After the acclimatization period fish was observed for 5 min and the number of horizontal and vertical midlines crossed, as well as the time spent in the shelter was observed. At the end of the first 5 min the weight was dropped into the tank and the fish was observed for another 5 min while the same behaviours were quantified (for detailed description of all behaviours noted see Table 2).



Figure 2.1.2: Observational tank for the simulated predator attack test

Table 2: Recorded behaviours for both personality trials- simulated predator attack (SPA), novel environment test (NE); with details of how scores were assigned.

SIMULATED PREDATOR ATTACK																																																									
Behavioural observation	Description																																																								
Total activity	Total number of vertical and horizontal line crosses before and after a weight was dropped into the observation tank.																																																								
Total time spent in a shelter (s)	Total time (out of 10 min) spent behind or directly in front of a shelter (plant). Values for before and after the weight was dropped were combined.																																																								
NOVEL ENVIRONMENT																																																									
Behavioural observation	Description																																																								
Time to enter the novel environment (s)	Time it took fish to enter the novel environment. The time was stopped when majority of the body crossed the door/novel environment interface. Fish that did not enter scored 10 minutes maximum time (600 s)																																																								
Number of times entered the novel environment	Number of times fish entered novel environment during the 10 min observational period.																																																								
Total time spent in the novel environment (s)	Duration of time fish spent in the novel environment out of 10 min.																																																								
Activity in the novel environment	Number of lines fish crossed in the novel environment during the 10 min observational period. Data was noted when majority of the body crossed the line.																																																								
Exploration index	<p>Each square was assign a value (1-3) depending on the distance from the door and the mean of those values was calculated producing the exploration index (see diagram below).</p> <div style="text-align: center;"> <table border="1" style="margin: 10px auto;"> <tr><td>49</td><td>50</td><td>51</td><td>52</td><td>53</td><td>54</td><td>55</td><td>56</td></tr> <tr><td>41</td><td>42</td><td>43</td><td>44</td><td>45</td><td>46</td><td>47</td><td>48</td></tr> <tr><td>33</td><td>34</td><td>35</td><td>36</td><td>37</td><td>38</td><td>39</td><td>40</td></tr> <tr><td>25</td><td>26</td><td>27</td><td>28</td><td>29</td><td>30</td><td>31</td><td>32</td></tr> <tr><td>17</td><td>18</td><td>19</td><td>20</td><td>21</td><td>22</td><td>23</td><td>24</td></tr> <tr><td>9</td><td>10</td><td>11</td><td>12</td><td>13</td><td>14</td><td>15</td><td>16</td></tr> <tr><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td><td>7</td><td>8</td></tr> </table> <div style="border: 1px solid black; padding: 5px; margin: 10px auto; width: fit-content;"> <p>1= pink 2= yellow 3= green</p> </div> </div>	49	50	51	52	53	54	55	56	41	42	43	44	45	46	47	48	33	34	35	36	37	38	39	40	25	26	27	28	29	30	31	32	17	18	19	20	21	22	23	24	9	10	11	12	13	14	15	16	1	2	3	4	5	6	7	8
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2.1.3: Repeated trials

A total of 745 fish was tested over a period of 8 weeks. To ensure consistency of behavioural response, both personality trials were re-tested on a subsample of 91 fish. Because of the large time difference between the earlier trials and later trials, the subsample of fish was chosen from fish tested either 14-16 weeks before the second testing (termed short term repeat) or 18-23 weeks before the second testing (termed long term repeat). In addition to choosing individuals based on the duration from the first personality testing, I also chose fish based on whether they entered the novel environment or not and based on their activity in the SPA test. As a result, the subsample of fish consisted of the following individuals:

- Long term repeat (repeated 18-23 weeks later)
 - 17 fish that did not enter novel environment
 - 32 fish that entered novel environment
- Short term repeat (repeated 14-16 weeks later)
 - 23 fish that did not enter novel environment
 - 19 fish that entered novel environment

The same methodology was used as for the first personality testing (see above). The colour of the gravel and of the plastic plants, as well as the colour of the walls were altered to reduce the risk of potential habituation by individual fish to the two personality tests (Jones & Godin 2010).

2.2: Group behaviours

Due to lack of correlation between the two personality tests (for detailed analysis see Results 3.1), the activity score and the amount of time spent in a shelter (both behaviours from the SPA test) were used to separate fish into two groups. The two behaviours are closely linked, meaning more active fish spent less time in the shelter and vice versa (for correlation between the two behaviours see Results 3.1); however in few cases fish were completely stationary outside of the shelter. Therefore, separating fish based on their activity levels and

shelter seeking was more appropriate. I named the categories “Passive” and “Active” and the actual data ranges for the two groups were as follows:

- PASSIVE
 - Total midline crossed 0-26
 - Time in shelter 205-600s
- ACTIVE
 - Total midline crossed 100-338
 - Time in shelter 0-327s

After the behaviour type of each fish was determined, fish were matched by size within 2mm (FL ranging 52.1 mm - 138.57 mm, average FL = 91.75 mm) and paired according to their behavioural type (in November 2012); either both Active (N = 26), or both Passive (N = 29). In addition, weight, length and depth were recorded. Each pair of fish was kept in 74 L flow-through aquarium (flow 5.45L/h, 100% water change in 12-13 hrs). Shelter and a plant were placed at the back of each experimental tank, covering ¼ of the bottom back portion of the tank. The back wall also contained an overflow pipe which was used as a hiding place by some fish and therefore was included as a shelter in the analysis. There was no gravel placed on the bottom of the tank to allow for easier removal of leftover food. Vertical and horizontal midlines were drawn on the outside of three walls of the tank and used to determine the level of activity. Tanks were screened off from visual disturbance and were placed behind a curtain on the shelf, alternating between Passive and Active to account for any disturbance created by people passing by the experimental area. Weight, but not depth and length, was recorded again in January 2013. Food was provided daily for a period of 2 months (starting in January 2013, previous to that fish were fed to satiation) in specialized feeders consisting of ice cube trays attached to a strip of plexiglass. The bottom of the tray was coated in gelatine and covered in koi carp granules (Foam et al. 2005). The feeders were placed at the front of the tank forcing carp to leave the shelter to feed. Feeders were left in the tank for two hours during which fish were undisturbed. After two hours feeders were removed and any leftover food siphoned out. Fish were fed 5% of their body weight, which was chosen based on preliminary feeding trial (see Appendix 1).

Group behavioural trials were commenced in February 2013. Each pair of fish was observed for 10 min and number of midlines crossed (activity) and time spent in the shelter were recorded. The average from the pair was used as a replicate. Observations were repeated

2 days later to investigate short term consistency in behaviours. At the end of the group behavioural trials (middle of March 2013) fish were weighed to the nearest mg and their fork length as well as their depth was measured again.

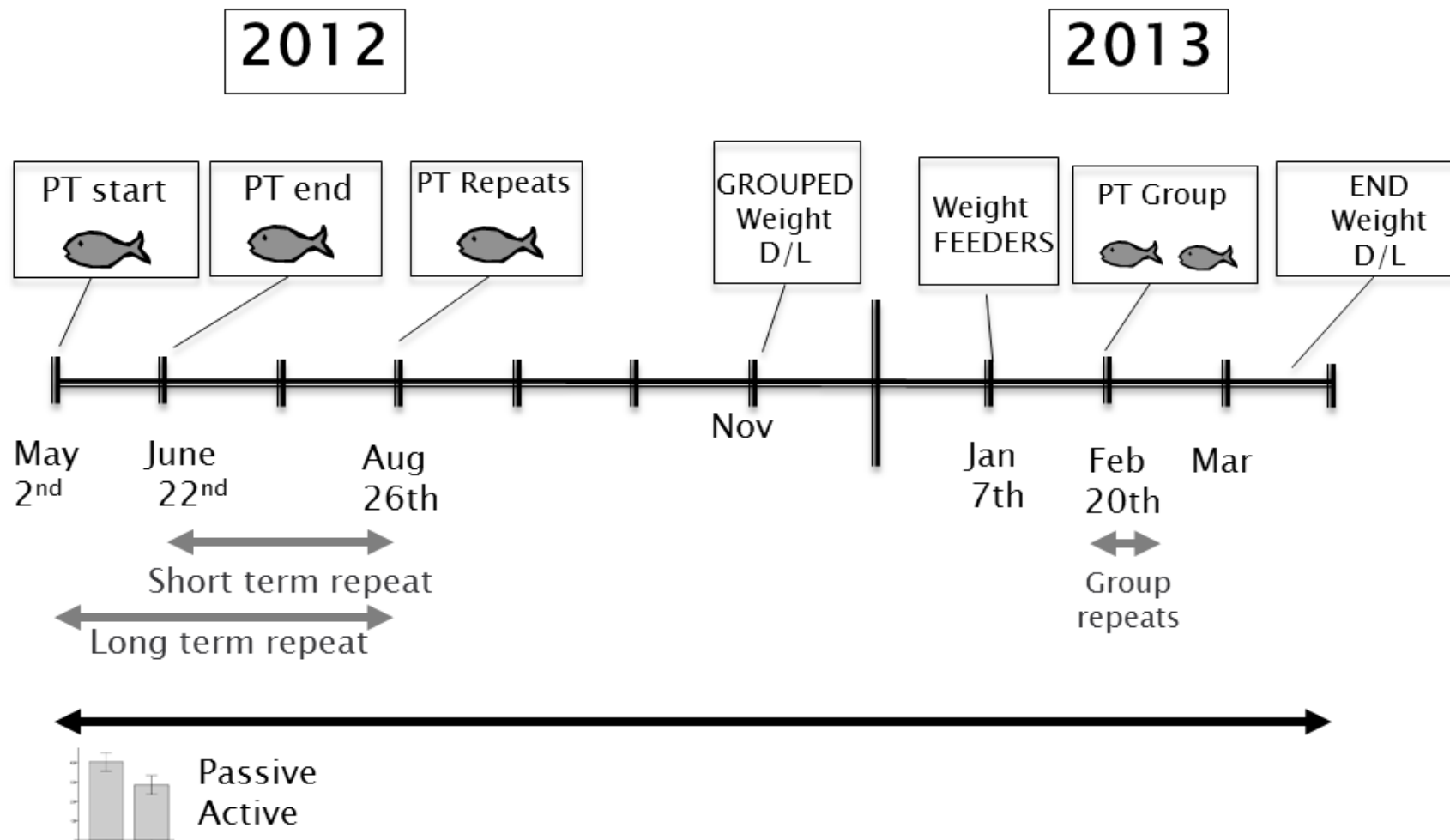


Figure 2.2: Timeline of the thesis work outlining the dates of each behavioural observation. Fish were categorized as Active or Passive based on their initial individual behavioural score which was used to analyse differences in group activity/shelter seeking, weight and D/L. PT = personality test.

2.3: Statistical analysis

All the statistical analysis was carried out in IBM SPSS Statistics, version 21.

2.3.1: Statistical analysis- Individual personality trials

I used principal component analysis (PCA) to summarize the five variables measured in the NE test (see Table 2) into one component called explorative tendency (Table 2.3.1). Non-parametric Spearman's rank correlation was then used to determine whether there is a relationship between the two variables from the SPA test (activity and time spent in shelter) and this new explorative tendency variable. However, because large majority of fish did not enter the novel environment (see Results bellow), the analysis was highly affected by the missing values from these individuals.

I used the same method to look only at those individuals that entered the novel environment to compare how the relationships change. Using PCA, I summarized the same five behaviours recorded in the NE test into two components. The first component was collectively called exploration and the following variables loaded heavily on the first axis: exploration index, time spent in the novel environment and activity in the novel environment. The second component was collectively called willingness to enter and variables that loaded heavily on the second axis were as follows: time to enter the novel environment and number of times entered (Table 2.3.2). In this case two components were needed to explain almost the same amount of variance as in the previous analysis (73.55% vs. 68.45%). Thus, when only those fish that entered the novel environment are analysed, the variables from the NE test are split into two distinct groups. The first group of variables described behaviours taking part after the fish entered the novel environment while the second group of variables described behaviours associated with the process of entering the novel environment. Similarly as above, the new variables were correlated with activity and times spent in shelter from the SPA test using non-parametric Spearman's rank correlation. Weight was also added into analyses to determine whether it affects any of the relationships observed.

Table 2.3.1: Principle component analysis on all data recorded in the initial novel environment tests

ALL DATA	
Behaviour	Component 1 (Explorative tendency) Loading
Time to enter the novel environment (s)	-0.842
Number of times entered the novel environment	0.845
Total time spent in the novel environment (s)	0.709
Activity in the novel environment	0.806
Exploration index	0.921
Cumulative variance explained (%)	68.45

Table 2.3.2: Principle component analysis on data recorded for fish that entered the novel environment.

DATA only including fish THAT ENTERED the novel environment		
Behaviour	Component 1 (Exploration) Loading	Component 2 (Willingness to enter) Loading
Time to enter the novel environment (s)	-0.057	0.765
Number of times entered the novel environment	0.227	-0.770
Total time spent in the novel environment (s)	0.880	0.051
Activity in the novel environment	0.909	-0.037
Exploration index	0.887	0.233
Cumulative variance explained (%)	48.826	24.723
Total variance explained (%)	73.55	

2.3.2: Statistical analysis- Repeated trials

Spearman's rank correlation was used to investigate whether activity and time spent in shelter from the first personality test were consistent when repeated on subsample of fish either 14-16 weeks (short term repeat) or 18-23 weeks (long term repeat) later.

Binomial logistic regression was also used to predict the likelihood of entering the novel environment again (dependent variable called tendency to enter 2; binary YES, NO). PCA was performed on variables from the initial SPA test and these variables were summarized into one component which was collectively called response to danger (Table 2.3.3). Higher score on this component indicated higher activity and lower time spent hiding in the shelter, while the opposite is indicated by lower PCA score. Response to danger and weight were used as covariates for regression analysis. In addition two categorical variables- tendency to enter 1 (binary YES, N = 51; NO, N = 40) and repeats (short term, N = 42; long term, N = 49)-were also used as covariates.

Table 2.3.3: Principle component analysis performed on data collected from the simulated predator attack test.

Simulated predator attack test	Component 1 (Response to danger) Loading
Activity	0.869
Time spent in shelter (s)	-0.869
Cumulative variance explained (%)	75.54

2.3.3: Statistical analysis- Group behaviours

Pearson’s correlations were used to investigate the relationship between group behaviours on day 1 and day 3. Where needed data were transformed using log or square root transformation to ensure the assumptions of the test are met. The average per tank (2 fish per tank) was calculated and used for analysis of group personality.

2.3.4: Statistical analysis- Linking individual personality with group personality

One-way Analysis of variance (ANOVA) was used to investigate whether there is a significant difference in time spent in shelter and activity between fish that were pre-determined as Passive or Active. Where needed data were either log transformed or square root transformed to meet the assumptions of the test.

2.3.5: Statistical analysis- weight and depth/length

One-way ANOVA was used to investigate whether there is a significant difference in weight in November, January and March as well as length and depth/length in November and March between fish that were pre-determined as Passive and Active. Separate Pearson's correlations were performed to investigate the relationship between group time spent in shelter and weight in January and March as well as depth/length in March. Where needed data were either log transformed or square root transformed to meet the assumptions of the test.

CHAPTER THREE: RESULTS

3.1: Individual personality trials

3.1.1: Correlations between SPA and NE variables

Out of 745 fish tested, 121 (1 in 6.5 fish) entered the novel environment. Several data points had to be removed due to the change in methodology, resulting in analysis of 657 fish, from which 89 entered the novel environment. As would be expected, activity and time spent in shelter (both variables from the SPA test) were significantly negatively correlated (see Table 3.1.1 for the r_s and P -values for all variables observed), meaning more active fish spent less time under the shelter. No correlation was observed between the behaviours collected in SPA test and explorative tendency- new variable combining all the behaviours from the NE test.

Table 3.1.1: The values of the Spearman's rank correlation coefficient (r_s) and P -values for all pairs of variables from the individual personality tests. Data for activity and time spent in shelter were collected from the SPA test; explorative tendency is a new variable combining behaviours collected from the NE test. $N = 657$

Behaviour	Correlated behaviours	r_s	P
Activity	Time spent in shelter (s)	-0.289**	<0.001
	Explorative tendency	-0.075	0.056
	Weight (g)	-0.072	0.064
Time spent in shelter (s)	Explorative tendency	0.063	0.108
	Weight (g)	0.066	0.090
Explorative tendency	Weight	0.054	0.170

** Correlation is significant at the 0.01 level, *Correlation is significant at the 0.05 level.

When only the fish that entered the novel environment were analysed the correlation between activity and time spent in shelter is still present (see Table 3.1.2 for the r_s and P -values for all pairs of variables), but again none of the variables from the different contexts

correlate with each other. However, a negative correlation was detected between activity and weight which was not detected before.

Table 3.1.2: The values of the Spearman's rank correlation coefficient (r_s) and P -values for all pairs of variables from the individual that entered the novel environment. Data for activity and time spent in shelter were collected from the SPA test, exploration and willingness to enter are new variables combining behaviours collected from the NE test. $N = 89$

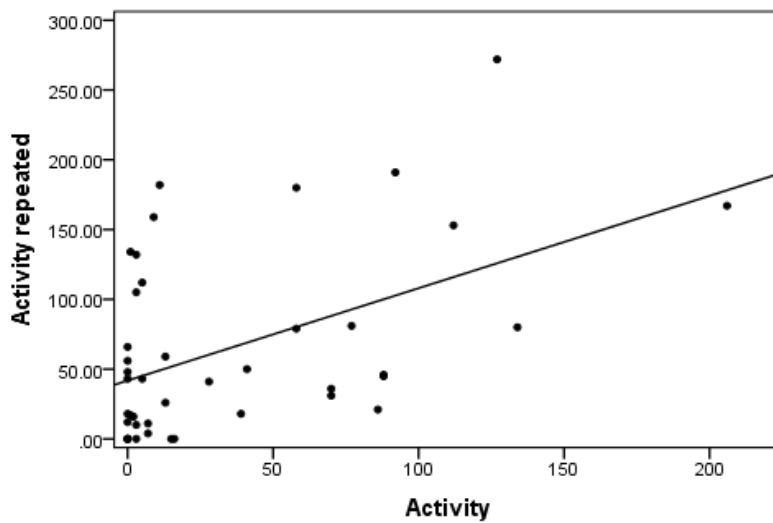
Behaviour	Correlated behaviours	r_s	P
Activity	Time spent in shelter (s)	-0.358**	0.001
	Exploration	-0.148	0.166
	Willingness to enter	-0.120	0.264
	Weight (g)	-0.273**	0.010
Time spent in shelter (s)	Exploration	-0.026	0.810
	Willingness to enter	0.076	0.481
	Weight (g)	0.010	0.927
Exploration	Willingness to enter	-0.193	0.070
	Weight (g)	0.007	0.951
Willingness to enter	Weight (g)	-0.120	0.263

** Correlation is significant at the 0.01 level, *Correlation is significant at the 0.05 level.

3.1.2: Repeated trials

Activity was not significantly correlated when measured again 18-23 weeks later (Spearman's correlation: $r_s = 0.161$, $N = 49$, $P = 0.269$, Figure 3.1.2b) but a significant correlation was found when the measure took place 14-16 weeks later (Spearman's correlation: $r_s = 0.426$, $N = 42$, $P = 0.005$, Figure 3.1.2a). Time in shelter was not consistent over either period of time (long term repeat: $r_s = -0.008$, $N = 49$, $P = 0.957$; short term repeat: $r_s = 0.223$, $N = 42$, $P = 0.156$).

a) Short term repeat



b) Long term repeat

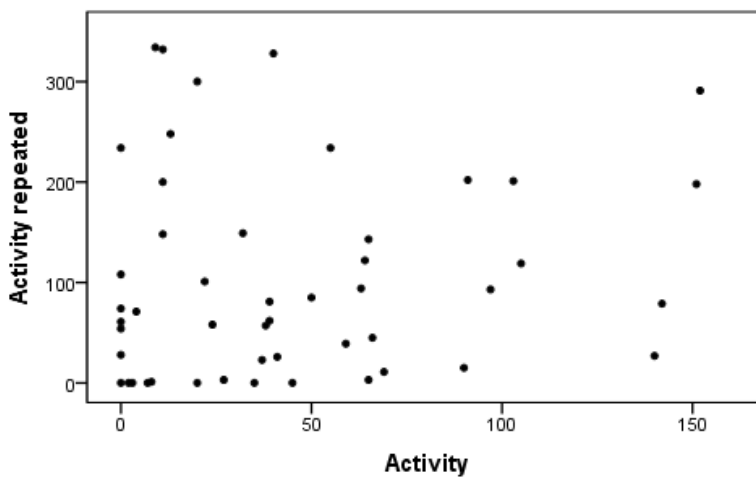


Figure 3.1.2: Correlation between Activity (measured as number of midline crossed) from the first personality trial and trial repeated 18-23 weeks later (Long term repeat; a) or 14-16 weeks later (Short term repeat; b).

A logistic regression analysis was conducted to predict whether fish enter the novel environment when subjected to the test again (tendency to enter 2). Stepwise backward logistic regression was used creating a minimally adequate model containing two predictors: tendency to enter 1 (binary; YES, NO) and response to danger. This model was statistically significant from the constant only model indicating that these variables as a set reliably

predict whether fish enters novel environment when tested again ($\chi^2 = 6.625$, $df = 2$, $P = 0.036$). Prediction success overall was 79.1% (97.1% for NO, fish will not enter again; 22.7% for YES, fish will enter again). The Wald criterion demonstrated that both tendency to enter 1 ($P = 0.037$) and response to danger ($P = 0.023$) made significant contribution to the prediction. Variables repeat (short vs. long, $P = 0.221$) and weight ($P = 0.406$) were non-significant predictors. The exponentiated B values for both variables are lower than 1 meaning that any increase in the predictors results in higher chance that fish will enter the novel environment.

Table 3.1.3: Summary of logistic regression analysis for variables significantly predicting the dependent variable called tendency to enter 2.

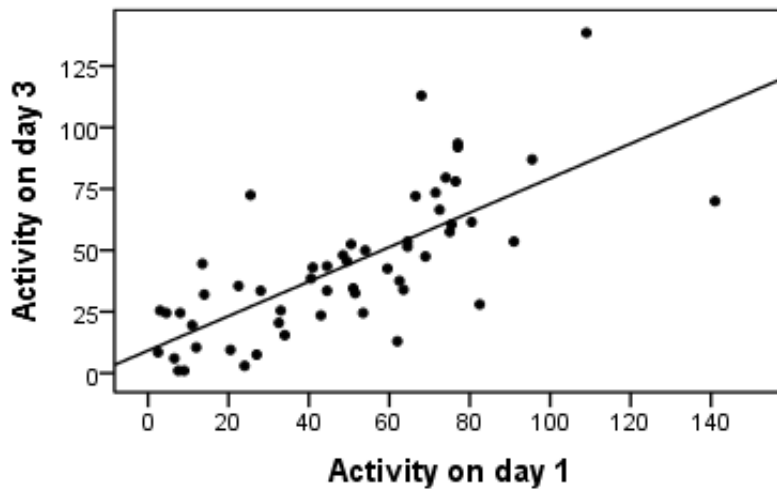
Predictor	B	$SE B$	Wald	df	P	e^B
Tendency to enter 1	-1.348	0.645	4.368	1	0.037	0.260
Response to danger	-0.808	0.354	5.198	1	0.023	0.446
Constant	-0.650	0.344	3.558	1	0.059	NA

Note: e^B = exponentiated B

3.2: Group personality trials

As would be expected both behaviours - activity and time spent in shelter- correlated with each other on the day of observation. Fish that were more active spent less time in a shelter on day 1 (Pearson correlation: $r = -0.352$, $N = 55$, $P = 0.008$) as well as two days later (Pearson correlation: $r = -0.395$, $N = 55$, $P = 0.003$). In addition, the time spent in a shelter on day 1 was correlated with the time spent in a shelter two days later (Pearson correlation: $r = 0.555$, $N = 55$, $P < 0.001$; Figure 3.2b). Similarly, activity on day 1 was significantly correlated with activity two days later (Pearson correlation: $r = 0.731$, $N = 55$, $P < 0.001$; Figure 3.2a). These observations support one of the personality assumptions that behaviours are consistent over time, in this case the time period being two days.

a)



b)

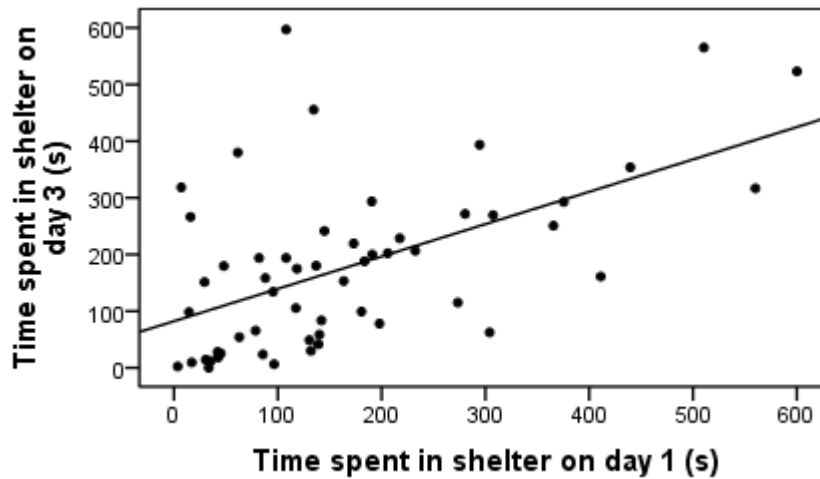


Figure 3.2: Correlation between group behaviours on day 1 and two days later. Activity (measured as number of midline crossed; a) and time spent in shelter (measured in seconds, b). Data shown are untransformed.

3.3: Linking data for individual personality and group personality

One-way ANOVA was performed to determine if there is a significant difference in time spent in shelter and activity between fish that were selected as Passive ($N = 29$) and fish that were selected as Active ($N = 26$) based on their results from the first individual personality trail. There was a significant difference in time spent in shelter between Passive and Active individuals ($F_{1,53} = 4.201$, $P = 0.045$) where Passive fish spent more time in the

shelter compared to Active fish (Fig 3.3.1). Activity, however, did not differ between the two personality groups ($F_{1,53} = 1.469, P = 0.231$).

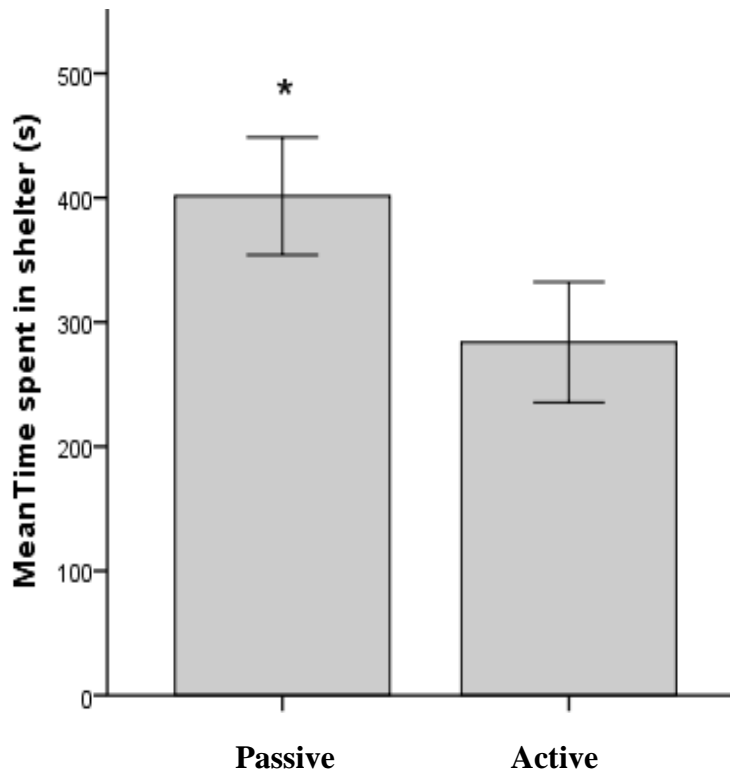


Figure 3.3.1: Mean time spent in shelter between fish that were pre-determined as Passive (N = 29) and Active (N = 26). Data (mean \pm SE) shown are untransformed.

3.4: Weight and depth/length

One-way ANOVA showed no significant difference in weight between Passive and Active fish in November ($F_{1,53} = 1.315, P = 0.257$), January ($F_{1,53} = 1.509, P = 0.225$), and March ($F_{1,53} = 1.117, P = 0.295$). Similarly no difference in length between Passive and Active fish was observed in November ($F_{1,53} = 1.435, P = 0.236$) or March ($F_{1,53} = 1.505, P = 0.225$). More detailed analysis using Pearson's correlation between the group time spent in shelter and weight in March showed almost significant negative relationship (Pearson correlation: $r = -0.256, N = 55, P = 0.059$; Fig 3.4.1) unlike in January where the relationship between time spent in a shelter and weight is weaker (Pearson correlation: $r = -0.218, N = 55, P = 0.109$). The correlation between time spent in shelter and average weight in March fails to be significant at the 0.05 level but it nicely demonstrates the relationship that would be

expected, where fish that spent more time in the shelter tend to weigh less than fish that spent less time in the shelter.

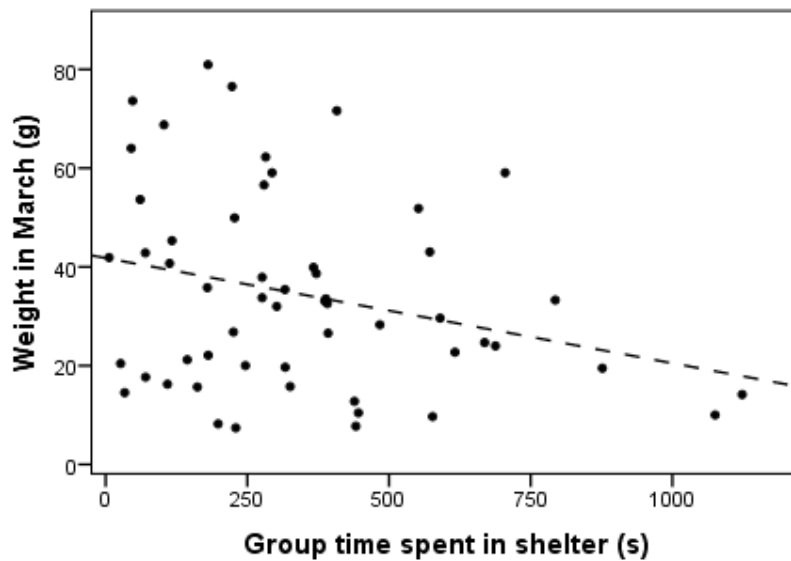


Figure 3.4.1: Correlation between group time spent in shelter and group weight in March. Data shown are untransformed. Dashed line outlines the slope of the nearly significant correlation ($P = 0.059$)

The depth/length did not differ between Passive and Active fish in November, right before they were grouped into their experimental tanks (November, $F_{1,53} = 1.489$, $P = 0.228$), but was significantly different at the end of the experiment (March, $F_{1,53} = 4.871$, $P = 0.032$) after fish were fed on specialized feeders for two months. Fish that were pre-determined as Active had significantly deeper bodies compared to Passive fish (Fig. 3.4.2). In addition Active fish also changed their depth/length between November and March significantly more compared to Passive fish ($F_{1,53} = 12.518$, $P = 0.001$). Interestingly, unlike the weight in March, the depth/length was not correlated with group time spent in shelter (Pearson correlation: $r = -0.216$, $N = 55$, $P = 0.113$) nor group activity (Pearson correlation: $r = -0.061$, $N = 55$, $P = 0.656$).

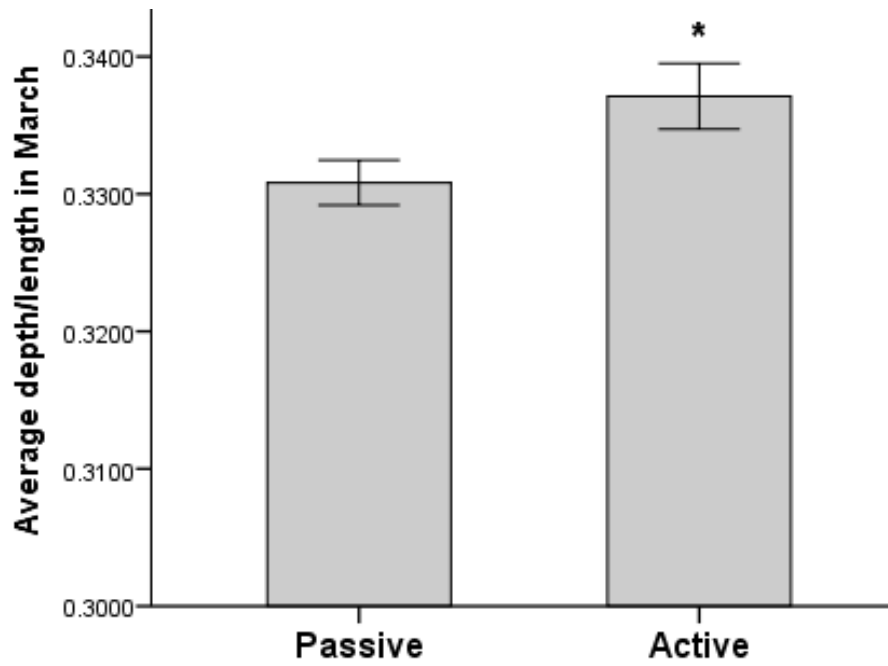


Figure 3.4.2: Mean depth/length at the end of the experiment between fish that were pre-determined as Passive (N = 29) and Active (N = 26). Data (mean \pm SE) shown are untransformed.

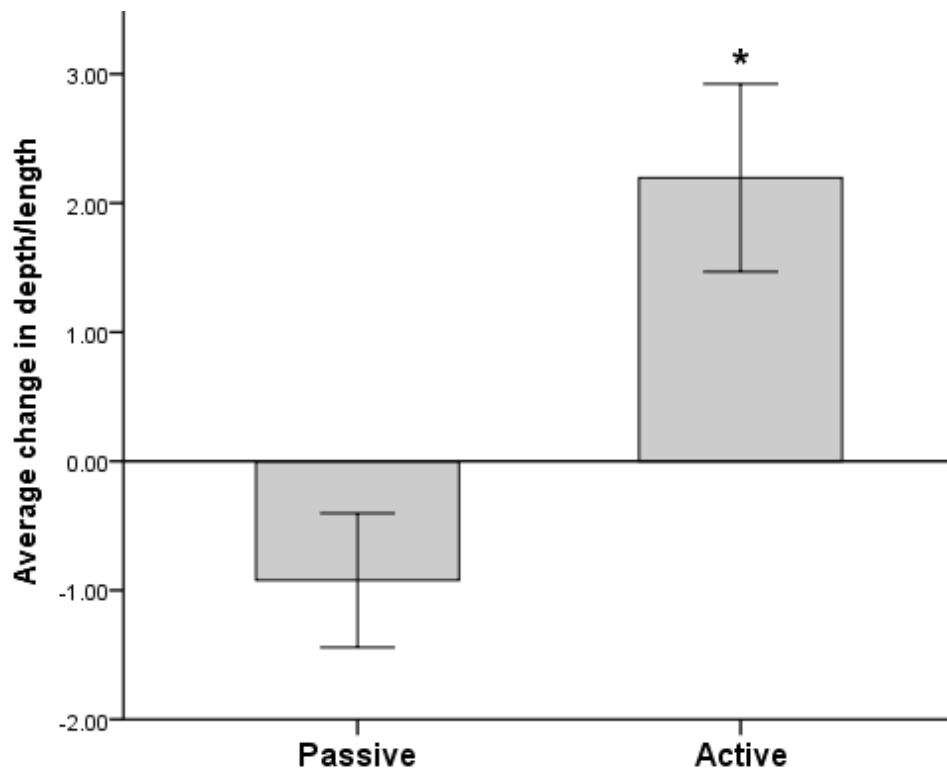


Figure 3.4.3: Mean change in depth/length between November and March in fish that were pre-determined as Passive (N = 29) and Active (N = 26). Data (mean \pm SE) shown are untransformed.

CHAPTER FOUR: DISCUSSION

4.1: Individual personality and the absence of behavioural syndrome

The results from the first part of my thesis showed no presence of behavioural syndrome, meaning there was no cross-situational consistency between behaviours from the two different personality tests - the novel environment test and the simulated predator attack test. The lack of correlation between behaviours is quite surprising. Conrad et al. (2011) summarized findings from existing literature documenting behavioural syndromes in fish, and in the majority of cases, boldness and exploration show positive correlation. The unwillingness of carp to enter the novel environment may be caused by inadequate acclimatization period. I have chosen 15 minute acclimatization based on the existing literature (Budaev et al. 1999; Ward et al. 2004; Huntingford et al. 2010) and to account for the time and space constraints related to such a large sample size (745 individuals tested overall). However, carp are shoaling fish and testing them individually as well as the relocation to a novel tank environment may be too stressful for juveniles. Huntingford et al. (2010) performed a similar novel environment test on common carp and encountered the same problem. They added food to the novel chamber to increase the willingness of carp to enter it, but by doing so, recorded behaviours may not be an accurate representation of exploration tendencies but rather of hunger levels. In addition, fish that did not enter the novel environment in their study were removed from analysis and re-tested the following day, possibly increasing the chance of habituation to the personality test.

Another explanation for the lack of behavioural correlation between two personality tests may be due to the absence of selection pressure. In both laboratory (Bell & Sih 2007) and natural (Adriaenssens & Johnsson 2013) settings, behavioural syndromes emerged after individuals were exposed to predation, but were not present before. Adaptive hypothesis predicts that behavioural syndromes should evolve only in populations where they are favoured by natural selection (Dingemanse et al. 2007). In several populations of sticklebacks the presence of behavioural syndrome between aggression, activity, and exploration (or boldness) existed only in environments with high predation pressure, while in the environments with low or no predation pressure, behavioural correlations were either

non-existent or very weak (Bell 2005; Dingemanse et al. 2007). Apart from the stress associated with personality testing, fish were not exposed to any threat stimulus for an extended period of time. My initial plan was to expose fish to predator odour for at least 2 months, after which I would subject individuals to the same personality tests to investigate the emergence of behavioural syndrome. Unfortunately, due to unforeseen circumstances I was not able to expose carp to predation threat. Interestingly, the component called response to danger (combining activity level and shelter seeking from the initial SPA test) was one of the significant variables predicting whether a fish enters the novel environment when tested again. This indicates that there might possibly be a weak relationship between behaviours from the different contexts.

4.2: Short term versus long term consistency in behaviours

Consistency of behaviours over time is an essential part of personality studies, thus the duration between tests is an important factor to consider when designing personality experiments. In the majority of cases, individuals are re-tested a few days (maximum few weeks) later to test for consistency in behaviours. The current study clearly demonstrates that consistency in behaviours over couple days does not necessarily imply consistency over a longer period of time. When re-tested two days later, group activity and time spent in a shelter were highly repeatable. The repeatability of behaviours could be enhanced by grouping fish by their activity score. When placed in groups, individuals may slightly modify their behaviours in response to the behaviours of their new group mates (Magnhagen and Staffan 2005). On many occasions, common carp were observed to follow each other in the experimental tank.

When the duration between the initial tests and repeated tests was increased the behavioural correlations were much weaker. Observations of individuals showed that activity (but not shelter seeking) recorded in the SPA test was repeatable when tested again 14 -16 weeks later, but no correlation was found for activity or shelter seeking when fish were tested 18 - 23 weeks later. A study investigating personality traits over ontogeny showed that behavioural stability depends on the stage in life history. Sinn et al. (2008) performed a lifetime (5 months) developmental study of shy/bold behaviour in dumpling squid *Euprymna tasmanica*. In this species, in-test individuals of shy/bold phenotypes were consistent during juvenile stage and after sexual maturity. During sexual maturation, however, apparent

behavioural re-organization took place and no consistency was observed in individual behaviours (Sinn et al. 2008). A time window may exist during which certain behaviours show a level of stability and the length of this window may be associated with major transitional periods in development. Wilson and Godin (2009) found only two out of four behaviours related to risk taking were repeatable 1-3 months later in the bluegill sunfish (*Lepomis macrochirus*). It is possible that a transitional period occurred between the time of short term repeats and long term repeats, after which activity was no longer consistent.

Individual activity and shelter seeking tendency from the initial SPA personality test were used to categorize fish into Active or Passive. While I found no significant difference in activity levels between Active and Passive carp, shelter seeking tendency differed between the two groups even after 10 months. Categorizing fish into Active and Passive was done by selecting individuals with extreme scores for activity and shelter use. Extreme phenotypes may be more likely to remain stable over time compared to intermediate phenotypes (Stamps & Groothuis 2010). From the two behaviours tested, activity may be more likely to change over long period of time. For example, fish can choose to be active or inactive but still remain outside of the shelter. Those fish may have slightly higher propensity to take risks since they chose not to stay hidden under the shelter. On the other hand, many of the Passive individuals spent all their time hiding under a shelter being completely inactive even before the weight was dropped into the tank, simulating the aerial predator attack. Those individuals were considered to be risk averse. Therefore, in comparison to activity, time spent in shelter may be more closely linked to risk-taking. Aside from increased risk-taking, shy individuals have, in general, higher shelter seeking tendency and spend less time in open habitat (Wilson et al. 1993; Wilson & McLaughlin 2007). Even though group behaviours were recorded when fish were undisturbed (in the morning), placing of the feeder into the tank created daily disturbance that could be perceived by carp as threat similar to the weight immersion in the SPA test. The long term repeatability of shelter seeking, but not activity, suggests that this behaviour is more ecologically or evolutionarily important when fish faced with potential predation event.

4.3: Body depth and weight

Behavioural correlations between activity and willingness to explore novel situations have been shown in several species of fish (three-spined stickleback, Dingemanse et al. 2007;

bluegill sunfish, Wilson & Godin 2009; mosquitofish (*Gambusia affinis*), Cote et al. 2010). For example, more active juvenile sunfish were also more likely to explore novel objects and take risks when confronted with a potential predation threat (Wilson & Godin 2009). Due to time constraints, I was not able to record any behaviour during the two hour feeding period. Behaviours associated with the willingness to approach the novel feeder, and the time spent feeding would provide more insight into the potential difference between Passive and Active fish. Placement of the feeder at the front of the tank (away from the shelter) caused an apparent disturbance to the fish. Feeders were placed into the tank for only 2 hours, constraining the time available for feeding. Therefore, fish had to rapidly approach the food after the feeder was placed into the tank to maximize their time spent feeding. The presence of a novel feeder, combined with the disturbance caused by placing the feeder into the experimental tank, could generate differences in feeding success between individuals with varying shelter seeking tendencies. Huntingford et al. (2010) provided evidence supporting the existence of a link between risk-taking and increased feeding opportunity in common carp. Despite the lack of significant difference in weight between Passive and Active fish at either point of the experiment, nearly significant negative correlation was found between weight at the end of the experiment and shelter seeking, meaning pairs of fish that tend to spend more time in a shelter were also more likely to weigh less at the end. Much weaker non-significant correlation was observed before the fish started to feed on the specialized feeders in January.

Change in body depth in response to a threat stimulus was reported in several species of fish, two of which, the goldfish (Chivers et al. 2008) and the crucian carp (Brönmark & Miner 1992), are close relatives to common carp used in this study. Common carp is an important aquaculture species in Europe and Asia (where it originates, Jhingran & Pullin 1985). Body shape, particularly the ratio of depth/length is regarded as an important feature of aquaculture-raised carp and high-backed carp (with larger depth/length ratio) are considered more aesthetic (Ankorion et al. 1992). As a consequence, research investigating the heritability of body depth for artificial selection is a main source of morphological studies in this species. To my knowledge, this is the first experiment investigating induced change in body depth in common carp from an ecological point of view.

The difference in body depth between Active and Passive fish without the presence of predator odour is intriguing. It is important to note that the depth/length difference was only found at the end of the experiment, after the fish were fed on the specialized feeders. Several

possible explanations exist to interpret the change in body depth without the presence of a chemical stimulus. The observed relationship could be linked to differential resource acquisition. A previous study showed that the extent to which fish exhibit induced morphological defences is influenced by the resource availability. Goldfish kept on a low food diet were less able to change their body depth when exposed to chemical alarm cues compared to individuals fed on high food diet (Chivers et al. 2008). In the absence of a pike predator, Brönmark & Miner (1992) detected marginal change in body depth in crucian carp kept on a high food diet when compared to carp fed on a low food diet. Similar morphological change in body depth was also shown in juvenile perch that were fed in excess (Borcherding & Magnhagen 2008). As I mentioned above, shelter seeking could be associated with risk aversion and tendency to avoid novelty, which in turn can be related to the ability to increase body depth. Active fish might be able to begin feeding sooner after the feeder is placed into the tank compared to Passive fish. This acquired energy can then be allocated to increase body depth.

Active and Passive fish may use differential strategies to cope with predation pressure. While Passive fish modify their behaviour and spend more time hiding in a shelter, Active fish use morphological defences to reduce predation pressure. Individuals possessing morphological defences should show reduced behavioural response when exposed to predation (Abrahams 1995). A support to this hypothesis was found in goldfish, where deep-bodied forms showed statistically lower intensity of behavioural antipredator response compared to shallow-bodied forms (Chivers et al. 2007). I propose that consistent individual differences in risk taking may generate different anti-predator adaptations in response to the threat created by placing of the feeder in the tank.

As pointed out in the introduction, both the type of diet and activity levels can influence body morphology in carp. In the study by Andersson et al. (2006), type of diet alone resulted in increased body depth in crucian carp. Having a deeper body is thought to be advantageous when feeding on benthic prey, as it allows for better manoeuvrability in the littoral zone. This prediction was confirmed in a study by Domenici et al. (2008) who reported that deep-bodied crucian carp had enhanced speed, acceleration, and turning rate compared to shallow-bodied carp. The specialized feeders used in this experiment may have a similar effect on body depth as benthic prey in the study performed by Andersson et al (2006). On several occasions I have observed carp in head down position and manoeuvring around the feeders during feeding attempts.

4.4: Future directions

Due to unfortunate circumstances I was not able to observe the development of personality under the threat of predation. Unsurprisingly, the next step would be to expose common carp to threat cues to determine whether the observed relationships become more pronounced. Studies by Bell and Sih (2007) and Adriaenssens and Johnsson (2013) showed that predation can induce emergence of behavioural syndromes. The next question that arises is: “Is the induced behavioural syndrome only a short term response or do these behavioural shifts persist for long period of time?”

Evidence suggests that predation promotes boldness in populations with naturally high predation (Brown et al. 2007). While fish exposed to constant predation pressure may have to accept higher predation threat and be more risk-prone in order to satisfy their foraging and reproductive needs, the scenario may be completely different when predation is one time event during a single stage in their life history. Embryos within the egg are capable of responding to water-borne chemicals which gives them an opportunity to acquire information about predators present in the environment (Warkentin 2011). My previous undergraduate work with zebrafish (*Danio rerio*) showed that behavioural differences between fish exposed to alarm cues as embryos and fish exposed to water control persist for as long as nine weeks. In this case, embryonically exposed fish were less aggressive and less successful in social contest than control fish (Vrtělová et al., unpublished data).

Only a handful of studies investigated the effect of embryonic exposure on the post-hatching behaviour in aquatic vertebrates (Saglio & Mandrillon 2006; Mathis et al. 2008). However, these studies tested behaviour immediately, or shortly after, hatching. Other environmental conditions during embryonic exposure are known to induce personality changes. Budaev and Andrew (2009) reported that development of zebrafish eggs and larvae in darkness induced shyness. In addition time of hatching also seems to affect the level of boldness in three-spined stickleback fry (Ruiz-Gomez & Huntingford 2012). Whether embryonic exposure to predation threat can induce similar changes in personality in aquatic species is unknown.

4.5: Conclusion

The definition of personality emphasizes the consistency of correlated behavioural traits over time. Yet, the amount of research looking into the stability of personality traits throughout the ontogeny of an individual is limited. The trade-offs associated with early life stages are different to those later in life. Individuals are much more vulnerable to predation in their early life stages, and different behavioural correlations may develop in young individuals compared to adults, where behaviours associated with mating and territoriality may be more important. Long term studies focusing on the change of personality traits through ontogeny represent a large and fruitful field in the current behavioural ecology. It seems that scientists have not reached a consensus on whether personality traits are fixed or flexible (Wilson & Krause 2012b) emphasizing the need for long term studies of personality through ontogeny.

I demonstrated that the stability of individual personality traits (in this case activity) can be time sensitive. Over a short period (several days), recorded behaviours show strong consistency, however, when the time window is increased the stability diminishes. Future research should carefully determine the time intervals between repeated trials depending on the questions that are being answered. More importantly, this research clearly emphasizes the need for long term studies.

In the second part of my thesis, I demonstrated for the first time the link between personality traits and induced morphological changes in fish. Less active fish with higher shelter seeking tendencies (Passive) developed more slender bodies compared to fish that were more active and spent less time in a shelter (Active). This relationship can be caused either by differences in feeding success, or by adoption of different anti-predator strategies. More research is needed to fully understand what causes the change in body depth in fish with different behavioural tendencies. Nevertheless, to observe these differences without the presence of chemical threat stimuli is fascinating.

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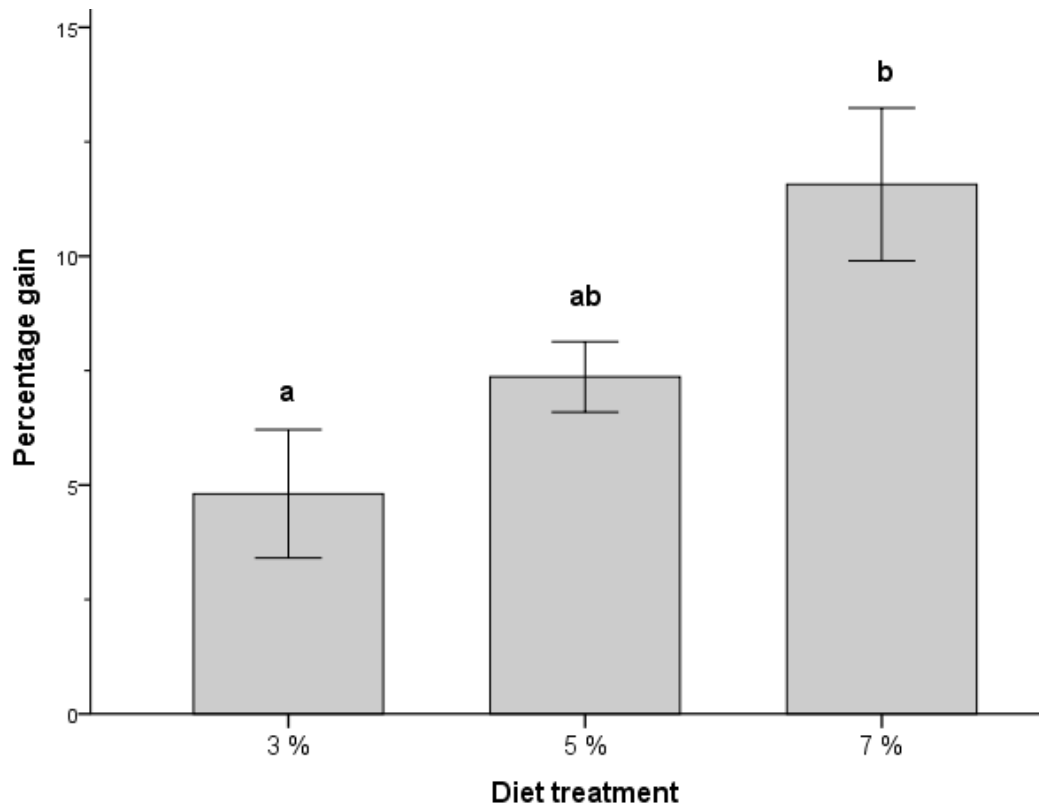
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Appendix 1

Feeding trial

It is crucial that common carp are fed the correct amount of food during their group trial period. The amount has to be low enough to encourage competition but enough to allow growth. Therefore a short feeding trial was run to determine what percentage of body weight is most adequate. Individual fish were weighed and move to 10 L tanks. Fish were fed daily one of three diets: 3%, 5% and 7% body weight provided on specialized feeders. One week later fish were re-weighed and the percentage weight gain was calculated. One-way ANOVA was performed to see whether there are differences in percentage weight gain between the three treatments. There was significant difference in percentage weight gain between treatments ($F_{2, 21} = 6.532$, $P = 0.006$). Fish fed 7% gained significantly more weight than fish fed 3% diet but not than fish fed 5% diet. There was no difference in percentage weight gain between fish fed 3% and fish fed 5% of their body weight (Appendix 1 Figure 1).



Appendix 1 Figure 1: Percentage weight gain (g) in fish kept on three diets: 3%, 5% and 7% body weight. Bars sharing a letter are not significantly different from one another (Tukey HSD, $P < 0.05$). Data shown are untransformed.