Causes and consequences of individual variation in anti-predator traits

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INTRODUCTION

Predators impose a potent evolutionary force on their prey, driving trait evolution and diversification of species and additionally predation can have powerful ecological consequences (Lima and Dill 1990, Lima 1998, Estes et al. 2011). Driven by intricacies in both predator and prey ecology, species differ in how they cope with their natural enemies and consequently, a huge range of anti-predator defences are displayed in nature (Edmunds 1974, Krause and Ruxton 2002, Caro 2005). Yet there is a growing recognition that, if we zoom into a certain species, or even into a single population of animals, there is still a huge and intriguing amount of individual trait variation (Bolnick et al. 2011, Chapman et al. 2011a, Brodersen et al. 2012). This recognition, along with recent advances in technology, have revolutionised the biological sciences, allowing us to study individual animals under natural or semi-natural conditions in many systems (Aarestrup et al. 2009, Vardanis et al. 2011, Brodersen et al. 2012, Dias et al. 2013, Hylander et al. 2014). Despite these recent advances, still little is known about the causes and consequences of individual phenotypic variation. In my thesis I address this gap in our knowledge, with a focus upon what drives individual variation in anti-predator traits, and the implications of this variation for individual animals.

Anti-predator defences

Predation escalates through a sequence of events (search, encounter, prey detection, attack, capture, ingestion) referred to as the predation sequence or cycle (Lima and Dill 1990, Jeschke 2008, Brönmark and Hansson 2012). Given that anti-predator defences of prey can operate to maximise survival at different stages in the sequence, a bewildering diversity of anti-predator defences are found in nature (Edmunds 1974, Lima and Dill 1990, Brönmark and Hansson 2012). Primary defences (e.g. camouflage, crypsis, reduced activity, spatial avoidance, migration, and refuge use) operate before the encounter with a potential enemy. If these primary defence mechanisms fail (i.e. prey are detected and identified by a predator) secondary defence mechanisms (e.g. escape mechanisms and evasive behaviours) may be deployed to escape an approaching enemy once detected. Finally, if a predator successfully captures their prey, tertiary defences may come into play during the prey-handling phase. These defences, which include elaborate morphological defensive structures such as horns and spines, specific body morphologies, venoms and toxins act to deter, repel and even induce mortality in the predator itself (Brodie and Brodie 1999).

Defence strategies versus predators can be either constitutive or inducible. Constitutive defences are traits always expressed by the host, regardless of the current risk of predation. However, many animals under variable predation risk have evolved plasticity in defence traits (Harvell 1990, Tollrian and Harvell 1999, Pigliucci 2001). Hence, rather than having permanent defences, phenotypically plastic prey with an inducible defence strategy respond only when required and can thus save costs when risk is low and the defence not needed. Inducible defences have been documented across a wide range of taxa and include morphological defences that make prey problematic or impossible for the predator to ingest (Nilsson et al. 1995, Tollrian and Harvell 1999). The other extreme includes inducible behavioural responses, which may result in spatial separation between the prey and its predator (Lima and Dill 1990, Brönmark and Hansson 2012). Hence individuals can vary both in which defensive traits or strategies they deploy against predators, but also in the degree to which defences are expressed, if the defences are phenotypically plastic.

In my thesis, I focus upon individual trait variation in defence strategies in two rather different study-systems. I first focus upon a classic and extreme example of phenotypic plasticity, and in **paper I,** explore what underlies interindividual variation in an induced morphological defence that makes crucian carp (*Carassius carassius*) less desirable prey for gape-limited predators. In **papers II- VI**, I explore various aspects of individuality in predation risk and migratory strategy, an anti-predator defence, in another common freshwater fish, the roach (*Rutilus rutilus*).

Individual trait variation

Biologists have long recognised that populations of animals in the wild consist of phenotypically diverse individuals that may differ in a range of traits, including morphology, behaviour and life history (Aristotle 350 BCE, Darwin 1859). More recently, it has also become evident that behavioural differences between individuals within populations can be consistent, with individual animals from a range of taxa having a tendency to behave in a predictable way. Hence, in addition to behavioural differences attributable to basic characteristics, such as gender, age and size, individuals may also express consistency over time and context for a wide range of behavioural traits including aggression, risk-taking, activity and exploration (Briffa and Weiss 2010, Mittelbach et al. 2014). This phenomenon, known as "animal personality", has attracted enormous interest from behavioural and evolutionary ecologists during the last decade (Bell 2007, Wolf et al. 2007). Hence, we now know individual-level personality-traits exist in a wide variety of animal taxa, including birds: (Dingemanse et al. 2003); reptiles: (Cote and Clobert 2007); fish: (Chapman et al. 2011b); insects: (Sih and Watters 2005); crustaceans: (Briffa et al. 2008). The perhaps most commonly investigated personality dimension is "boldness", i.e. behavioural variation along the bold–shy continuum (Wilson et al. 1993). According to this major axis of animal personality, individuals within and between populations differ in their propensity to take risks, with bold individuals being consistently more prone to engage in risky behaviour, whereas shy individuals are consistently more risk averse and cautious (Wilson et al. 1994). To persist in natural populations of animals over long periods of time, consistent differences in personality-like characteristics must have an equivalent fitness pay-off, and hence documenting the costs and benefits associated with divergent behavioural types is a contemporary challenge in modern behavioural ecology (Frost et al. 2007). A central axiom of many of the discussions surrounding the evolution of animal personality is that individuals with divergent behavioural types differ in a cost-benefit trade-off where animals with risk-prone personalities (bold individuals) access greater rewards including resources and mates, but at the cost of exposure to higher risk, such as predation (Biro et al. 2004, Smith and Blumstein 2008, Sih and Del Giudice 2012). If boldness has a negative bearing upon the predation vulnerability of a given individual one might predict bold individuals may benefit more than shy individuals from investing in compensatory strategies (the "phenotypic compensation hypothesis") at various stages in the predation sequence to minimise the costs associated with this personality type (Hulthén et al. 2014b). I explore links between personality types, predation risk and risk-reducing strategies in **paper I, II, and III**.

STUDY SYSTEM I

Phenotypic plasticity and inducible defences

Phenotypic plasticity is generally defined as the ability of individual genotypes to modify its phenotype in response to being exposed to different environmental conditions (Pigliucci 2005). As previously mentioned, many animals under variable predation risk have evolved plasticity in their defence traits (Tollrian and Harvell 1999, Pigliucci 2001, 2005). Prey with an inducible defence strategy respond only when required (i.e. in a scenario of increased risk) which allows for allocation costs to be saved when risk is low or predators are absent (Harvell 1990, Tollrian and Harvell 1999). Studies on inducible defences have typically focused on trait means (i.e. the average response of treatment groups versus a control), rather than focusing on the magnitude of trait changes of individual animals. However, even within populations, physiological constraints vary between individuals, and furthermore the risk of predation is not necessarily equally shared across all members, and there may be considerable interindividual variation in the degree to which defences are expressed. Although this variation is intriguingly documented in studies of inducible defences, it remains poorly understood, and rarely studied explicitly as a stand-alone phenomenon.

Morphological defence in crucian carp

The extreme phenotypic plasticity in body shape found in crucian carp constitutes a textbook example of a defence that operates during attack and capture. When exposed to chemical cues released by piscivorous predators, such as pike (*Esox lucius*), crucians respond by a drastic increase in body depth (Brönmark and Miner 1992). The morphologically defended phenotype is a less desirable prey for predators constrained by their gape-size (Nilsson et al. 1995, Nilsson and Brönmark 2000). Furthermore, the deep body has been shown to improve escape performance via enhanced locomotor capacity (Domenici et al. 2008). However, morphologically defended carps (i.e. deep-bodied) experience higher drag and experience density dependent costs when competing with undefended (shallow-bodied) carps (Pettersson and Brönmark 1999). Hence, one might predict that selection should favour more effective defences in more vulnerable individuals where paying such costs is worthwhile. As boldness is thought to be linked to an increase in individual risk, I tested the hypothesis that individuals showing risky behaviours (bold individuals) exhibit trait compensation (offset the costs of one trait by the benefits of another; Rundle and

Brönmark 2001) by expressing enhanced morphological defences in **paper I.**

STUDY SYSTEM II

Animal migration

Out of all animal movement phenomena in nature, migratory behaviour certainly constitutes one of the most visible and spectacular. Birds are the iconic migrants, and as such they have received a great deal of attention and been the subjects of numerous empirical and theoretical studies, making the current body of literature biased towards patterns of avian migration. Nevertheless, migratory behaviour is exceptionally widespread and spans taxa as diverse as mammals, fish, amphibians, crustaceans, reptiles and insects (Dingle 1996, Brönmark et al. 2013, Hansson and Åkesson 2014). If one looks across taxa it is apparent that migratory movements may take a variety of forms. Associated with extreme physiological demands and great hardships are the spectacular journeys of for example Artic terns (*Sterna paradisaea*), bar-tailed godwits (*Limosa lapponica),* and European eels *(Anguilla anguilla*). These extreme endurance migrants have the capacity to migrate more than 80,000 km annually, fly 11,000 km non-stop or undertake a trans-Atlantic migration in a fasting state (Gill et al. 2005, van Ginneken et al. 2005, Egevang et al. 2010). The diversity of migratory behaviour in the animal kingdom is further emphasised by the fact that migratory cycles can range from a few metres in amplitude and be completed within a few hours (diel vertical migration in e.g. zooplankton and fish), or require several generations of animals to be fulfilled, as exemplified by the spectacular monarch butterfly migration (Wassenaar and Hobson 1998, Mehner 2012, Hylander et al. 2014). Researchers of migratory behaviour have undoubtedly been successful in their efforts to shed new light upon the mystery of migration. We now know that animal migration may have far-reaching implications for the fitness of individual migrants, but also for the functioning of entire ecosystems (Nathan et al. 2008, Bauer and Hoye 2014, Hansson and Åkesson 2014). We have gained important insights into why many animals migrate, which routes they use and how they navigate to reach their destinations (Hansson and Åkesson 2014). In addition, we know that migratory animals are finely tuned to meet the requirements of migration with specific adaptations involving morphological, physiological and behavioural traits (Dingle 2006, Ramenofsky and Wingfield 2007). However, migration ecologists still have an important role to play as important pieces to the puzzle of migration are still missing and may be urgently needed. The rapid progression of human-induced habitat disturbance, including fragmentation, climate change and overexploitation, has raised concerns about migratory animals becoming increasingly endangered (Wilcove 2011). A more comprehensive understanding of the processes that underlie migratory behaviour is hence much needed since it will provide the framework for conservation of these species (Wilcove and Wikelski 2008).

Why do animals migrate?

The primary drivers that underlie migratory behaviour remain a hotly debated subject. Migration often occurs in synchrony with seasonal changes in the environment and with a high degree of temporal regularity and predictability (Fryxell and Sinclair 1988). Hence, migration is most often recognised as a behavioural strategy to maximise fitness in seasonal environments (Alerstam et al. 2003). Migration thus allows numerous animals in nature to exploit resources available only part of the year or in certain habitats (e.g. food, optimal climates) and/or avoid competition, adverse environmental conditions, parasites and predation (McKinnon et al. 2010, Altizer et al. 2011, Skov et al. 2013, Hansson and Åkesson 2014).

Individual variation in migration (a.k.a. partial/differential migration)

It has been increasingly evident that alternative strategies coexist within many migratory populations. Members of the same population often differ considerably in their timing, destination and propensity to migrate, and the terms partial and differential migration are widely used to describe such migratory diversity (Ketterson and Nolan 1983, Chapman et al. 2011a). In partial migration, only some individuals partake in migratory behaviour whilst others remain resident, (Lack 1943, Chapman et al. 2011a). Partial migration with individual-specific life histories is probably the most common form of migration, and has been widely reported in numerous taxa, including invertebrates, fish, birds amphibians, and mammals (Chapman et al. 2011a, Chapman et al. 2012). Scientists have long strived to get a more cohesive understanding of the ultimate factors underlying migratory decisions at the individual level, a question that has remained a challenge for migration ecologists. However, since partial migration likely represents a stage of evolutionary transition between residency and complete migration (Berthold 1999), partially migratory species are particularly promising candidates for successfully addressing such questions (Boyle 2008). In addition, coexisting alternative migration strategies and the spatial segregation of migrants and resident offers a unique opportunity for comparative studies where traits associated with migration and residency can be identified. Yet despite this potential, partial migration remains a relatively understudied form of migration (Sekercioglu 2010, Chapman et al. 2011a). Although partial migration may take a variety of forms (see Chapman et al. 2011a), in my study system conspecifics share a breeding site but segregate spatially when part of the population migrate to winter elsewhere. This type, referred to as ‘non-breeding partial migration’ is arguably the most common form of partial migration in nature, documented across a wide taxonomic breadth (Chapman et al. 2011a). Moreover, this type may be *facultative* such that the expression of migratory and sedentary life-histories covary with prevailing conditions and the current state of individuals (Olsson et al. 2006, Brodersen et al. 2008, Ogonowski and Conway 2009), or *obligate* where migratory tactics are more fixed and under genetic control (Berthold 1991).

The control of partial migration

Several explanations and general theories have been put forward to explain partial migration and most of them have focused on the classical scenario where migrants and residents breed together but overwinter apart (Cohen 1967, Lundberg 1987, Kaitala et al. 1993). First, the coexistence of migratory and non-migratory behaviours may be genetically controlled through parental bet hedging or genetic dimorphism (Berthold and Querner 1982, Biebach 1983). Secondly, early and pioneering theory on partial migration also recognised that partial migration in both avian and fish migrants may be explained as a mixed evolutionary stable strategy arising from frequency-dependent selection (Lundberg 1988, Kaitala et al. 1993, Gross 1996). Finally, partial migration may have evolved as a conditional strategy, in which the adoption of resident or migratory life history strategies depends upon individual states, such as age, sex, dominance status or body condition (Brodersen et al. 2008, Grayson and Wilbur 2009). In recent years it has become increasingly evident that migration often is condition dependent and that environmental factors may be very influential for controlling patterns of partial migration (Ogonowski and Conway 2009). Accordingly, flexibility and phenotypic plasticity in migratory behaviour has been demonstrated in a number of species in response to various ecological factors. For example, Grayson and Wilbur (2009), provided evidence for environmentally induced migration in red-spotted newts by experimental manipulation of population density and sex ratio in aquatic field enclosures and the migratory propensity of tropical manakins is influenced by storm events (Boyle et al. 2010). Elegant experimental work has also highlighted the flexibility of a range of migratory traits in fishes in response to feeding conditions. For example, in a landmark study, Olsson et al. (2006), reciprocally transplanted trout (*Salmo trutta*) between river sections that differed in conspecific density and hence growth opportunities. Transplantation into high-density conditions promoted migratory behaviour whereas transplantation into low-density river sections favoured residency. Subsequent food manipulation trials in the laboratory also revealed that trout reared under low food conditions were more likely to develop the migratory phenotype (Olsson et al. 2006, Wysujack et al. 2009). Another study showed that the propensity of roach to migrate could be modified by manipulating feeding conditions prior to the onset of migration, with fish in experimentally induced poor condition displaying a lower tendency to migrate (Brodersen et al. 2008, Brodersen et al. 2014). Hence, whilst food conditions prior to migration seems to influence migratory decisions in a number of cases, few studies have investigated how experience of predation risk influences migratory propensity in the wild. I address the role of experimentally manipulated risk on migratory decisions in **paper IV.**

Partial migration in cyprinid fish

Seasonal migration by cyprinid fish (Fig. 1) has been reported from freshwater lakes all over Europe (Jordan and Wortley 1985, Borcherding et al. 2002, Jepsen and Berg 2002, Heermann and Borcherding 2006, Skov et al. 2010). The migratory patterns of cyprinids are not uniform between species and populations. For example, in some cases cyprinids undertake migrations during the summer months with the purpose to spawn or feed (L'Abée-Lund and Vøllestad 1987), whereas other populations migrate seasonally in step with changes in resource

Fig. 1. Cyprinid fish start to leave our study lakes on behalf of connected streams during early autumn and when winter's grip is firm, thousands upon thousands of fish resides in the streams [Photo: Aron Hejdström]

availability relative to predation risk (Brönmark et al. 2008). The latter form has received the most attention and is the subject of my thesis. Our study lakes are small, shallow and moderately eutrophic lakes situated in southern Sweden and southern Jutland, Denmark, respectively. Our model organism, roach (*Rutilus rutilus*), a common freshwater fish and a partial migrant, start to leave the lakes via connected streams during early autumn, and a significant fraction (up to *c* 70%) of the roach population resides in the streams when winter's grip is firm, whereas other individual remain as residents in the lake year-round. The stream wintering grounds hold low densities of stationary piscivorous predators and the vast majority of the pike populations in the lakes do not follow the migratory prey into the stream habitat (Skov et al. 2008, Skov et al. 2011). Recent theoretical work suggests that the roach migration is governed by seasonal changes to a growth-mortality trade-off, which I will explore in the following section.

The growth-mortality trade-off

Virtually all animals in nature constitute potential prey, and as such they are frequently faced with trade-offs, including finding a balance between acquiring resources for growth, whilst avoiding their natural enemies (Werner and Anholt 1993, McPeek 2004). To cope with this fundamental trade-off prey can modify their behaviour (Lima and Dill 1990), and, for example, decrease foraging rates to reduce the exposure to potential predators. In addition, because food abundance and predation risk often vary over a spatiotemporal scale, mobile animals also have the opportunity to mediate the trade-off by making habitat shifts (Gilliam and Fraser 1987). For example, diel vertical migration (DVM), with ascents and descents during crepuscular periods allows juvenile sockeye salmon (*Oncorhynchus nerka*) and coregonids (*Coregonus spp*) to actively forage during periods of low light intensity (referred to as the "anti-predation window"), and thus reduce the risk of being predated by visually oriented predators (Scheuerell and Schindler 2003, Mehner and Kasprzak 2011). However, relatively few studies have investigated the role of growth - mortality trade-offs for shaping patterns of migration in fish over longer time scales (i.e. seasonal migration). Building on the previous theoretical framework of Werner and Gilliam (1984), a conceptual model for the timing of seasonal migration in roach (Fig. 2) was recently developed by Brönmark et al. (2008) with the rationale that migration should coincide with temperature-driven changes in the ratio between predation risk (P) and growth potential (G). Food availability and the activity of lake-dwelling piscivorous fish are positively correlated with temperature. Temperature declines, owing to the seasonal cycle, are therefore accompanied by a decrease in both food availability and mortality risk for roach. Whilst zooplankton, the principle contributor to the roach diet, decline in abundance to be virtually absent during the coldest months, predatory fish continue to be active and feed, albeit less frequently due to reduced metabolism (Frost 1954, Baktoft et al. 2012). Streams connected to the lake offer a habitat with low density of predatory fish, but also a low food supply relative to the lake (Skov et al. 2008). The ratio between predation risk and growth potential therefore becomes relatively higher in the lake with seasonally decreasing temperatures. Via migration, roach can avoid habitats with high risk during periods of low growth (Fig. 2). The actual migration patterns of wild, individually tracked roach follows the model predictions with a remarkable accuracy (Brönmark et al. 2008). Empirical evidence also supports the axioms of the P/G model: migrants benefit from a reduced predation risk from avian predators by refuging in the low risk streams during winter (Skov et al. 2013), whilst paying a foraging cost by migrating to a relatively food-poor habitat (Chapman et al. 2013). Although the model gives insights into both when and why animals may migrate it does not explain why individual differ in migratory pattern and tendency (i.e. why is the migration only partial?). However, as previously mentioned, animals may differ in a range of traits, which in turn may affect growth potential, and predation risk at the level of individuals. Thus, the cost / benefit analysis of remaining resident in the lake vs. undertake a migration to low-risk habitats may differ as a function of individual risk-taking (boldness) mediated by predation vulnerability. I test the prediction that bold individuals are more vulnerable to predation and benefit more from migration away from natural enemies during periods of low food availability in **paper II and III.**

METHODS TO STUDY INDIVIDUAL TRAIT VARIATION

PIT-tags and RFID technology

Although my thesis is relatively diverse, the use of PIT-tags and Radio Frequency Identification (RFID) is a methodological

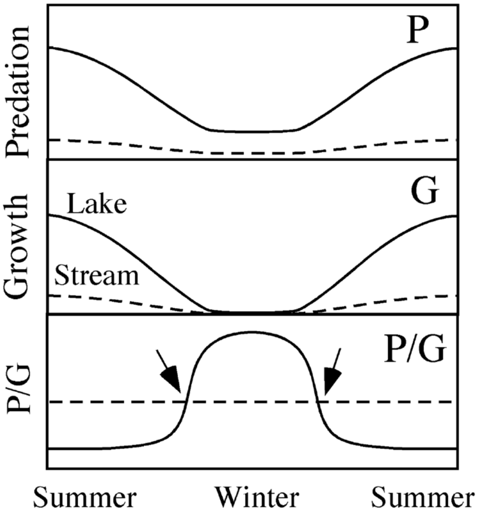

Fig. 2. A conceptual model for seasonal changes in predation rate by piscivores, growth rate in zooplanktivorous fish and the trade-off, i.e. the ratio of predation and growth, in the lake and stream habitat. Migrating roach are expected to change habitat so that they minimize the ratio and, thus, migrate from the lake to the stream in autumn and back to the lake in spring, as indicated by arrows. Brönmark et al 2008 (*PLoS ONE*).

feature shared across all my chapters. PIT-tags are small electronic microchips encapsulated in biocompatible glass (Fig. 3a) that can be surgically inserted body into the body cavity of fishes. The tags has no internal battery, but are instead activated by an external electromagnetic field to activate the transmission of a unique identity code which is then recorded on a reader (portable or stationary). Hence, once implanted they provide a reliable "lifetime" barcode for individual animals. Laboratory and field experiments have revealed that the PIT-tagging of cyprinids has no measurable effects on survival, behaviour or body-condition (Skov et al. 2005, Hulthén et al. 2014a). These uniquely coded electronic tags can be used in laboratory settings in combination with a hand-held scanner (Fig. 3b), which allowed us to keep track of and document trait changes (morphology and behaviour) of each individual during the entire experiment **in paper I.** In addition, these tags have played a central role for my thesis as I have used them to document predation events on individual animals (**paper III**), and to document migratory behaviour in the wild (**paper II, IV, V, VI**). Migration in our study systems occurs along well-defined routes (streams are rarely more than 4 meters wide and 60 centimetres deep), which allow in-stream monitoring using paired, fixed-location antennas (Fig. 3c). Fish are caught in the lake habitat and tagged with PIT-tags. Stationary and continuously operating PIT-tag detection systems are installed in the connected inlet and outlets of our study lakes. The system in each stream consists of two loop-shaped antennas, each covering the entire cross- section of the stream. Each antenna is connected to a tuning module, which in turn is wired to a central RFID multiplexer unit. When a tagged fish swims through or in the vicinity of an antenna, the PIT-tag is energised and emits a unique code. The reader records and stores all tag detections together with a date and time stamp on a memory card. The use of two sequential antennae enables determination of fish swimming direction. Finally, I take advantage of the tags and a natural history quirk in one of our predator species (cormorants; *Phalacrocorax carbo* spp.) Cormorants feed on tagged fish and regurgitate fully functioning tags at their roost in the lake. By ascertaining the identity of cormorant-killed individuals (by using portable detectors at the roost) I were able to relate

Fig. 3. (a) Passive integrated transponders (PIT) tags can be implanted into the body cavity of fish [Photo: Oregon RFID] (b) the microchip sends a unique, numeric code that can be read by a hand-held scanner [Photo: Aron Hejdström] (c) or a pass-through PIT-tag antenna system in the field that records the identity code and a date and time stamp of migrating fish [Photo: Kaj Hulthén].

individual prey boldness to the probability of a known predation event in **paper III.**

SUMMARY OF PAPERS I-VI

Objectives

The general objectives of this thesis are to investigate the causes and consequences of individual trait variation in predator defences in two contrasting systems: the inducible defences of the crucian carp and the over-winter migration of the roach.

Specifically, I ask the following questions:

- Do animals with bold personality types engage in compensatory strategies (morphological defence induction or over-winter migration) to minimise the potential costs (increased predation risk) associated with this personality type? (**Paper I**, and **II**).
- Is behaviour influenced by predator exposure (**Papers I and IV**) and are there differences in behavioural plasticity between shy/bold phenotypes? (**Paper I**)**.**
- Do bold individuals pay a higher predation cost than individuals that adopt a risk-averse behavioural strategy? (**Paper III**).
- Can seasonal migrants adjust their migratory behaviour based on the perception of predation risk, i.e. through previous experience? **(Paper IV).**
- Does temporal variation in migratory timing differ between seasons (i.e. autumn and spring) and is migratory timing at an individual level related to survival (i.e. is timing under selection)? **(Paper V).**
- Can variation in body morphology within a species be explained by variation in migratory strategy (migration/residency)? **(Paper VI).**

Methods summary

To elucidate if boldness is a driver of between-individual variation in anti-predator defences (**Paper I**), I caught wild crucian carp naive to predation (i.e. of shallow-bodied morphology). Thereafter, all fish were individually tagged, acclimatised for four weeks and assayed for individual boldness. I used a standard refuge emergence protocol (latency to emerge from a refuge box) to obtain a boldness score and each individual were assayed twice. Consistently bold and consistently shy individuals were then assigned to experimental tanks in groups of three individuals (of either bold or shy personality). Experimental tanks were randomly assigned to treatments in a factorial design with the factors pike (presence/absence) and personality type (bold/shy) and each treatment combination was replicated five times. After approximately four months of treatment exposure, all carps were re-assayed for boldness and I assessed individual change in maximum body depth, weight and boldness over the experimental period. In addition to morphological defences, animals can also avoid being captured by their natural enemies by investing in a migratory strategy. To investigate the influence of boldness upon migratory propensity (**paper II**), roach were caught from the partially migratory population in lake Krankesjön during two consecutive years (2009 and 2010). Captured fish were transported to experimental facilities at Lund University, acclimatised for one week and then, assayed for individual boldness according to the protocol described previously. Next, all fish were individually PIT-tagged and transported back to the lake were they were released at the approximate location of capture. We then monitored migration between the lake and the connected stream using stationary, continuously operating antenna arrays in the streams connected to our study lakes. In **paper II**, we speculated that one explanation for why bold fish have a higher migration propensity is that they have higher predation vulnerability due to their risk-prone behaviour. In **paper III,** I was able to test the prediction that predators select against boldness. Cormorants prey upon tagged fish and regurgitate fully functioning PIT-tags at a well-defined roost in our study lake. After allowing for *c* 2.5 – 3.5 years of natural predation in the wild on these individuals with a known degree of boldness I collected tag data from predated fish using portable detectors at the cormorant roost. Hence, by ascertaining the identity of cormorant-killed individuals I were able to relate individual prey boldness to the probability of a known predation event over several years of predation by a key avian predator in a natural predator-prey system. As previously mentioned, recent theoretical work suggest that seasonal changes to a predation/growth potential (P/G) trade-off between the lake and stream habitat is key in shaping migratory dynamics in my model organism. Therefore, I wanted to empirically test if individual migration propensity can be a plastic behavioural response influenced by perceived predation risk **(Paper IV)**. To achieve this I combined controlled exposure experiments, where I manipulated individuals' perception of current predation risk with field monitoring of their subsequent post-exposure migratory behaviour. The direct perceived risk of roach was experimentally manipulated by exposing them to presence or absence of their natural predator (pike), in large experimental mesocosms prior to the migratory period**.** I also manipulated indirect perceived risk, by modifying the group size (high and low-density). Next, I released all fish to their lake of origin (Krankesjön) and monitored their treatment-dependent migration propensities using our PIT-tag antenna system. Appropriate timing is generally regarded as a key to migratory success, particularly in environments like our temperate lake study-system where the relative costs and benefits of the lake as a habitat for roach fish have a strong seasonal pattern. In **paper V**, I aimed to explore temporal patterns and variance in migratory timing and ask whether timing is related to survival (i.e. under selection). To achieve this, I explored a long-term data set gathered by individual based tracking of roach in two European lakes over multiple migration periods (10 and 8 years respectively.) This highly detailed data set (year-round scheduling and repeat journeys of the same individual) allowed me to analyse migratory patterns of both populations and individuals. Finally, I explored morphological correlates of migration and investigated if variation in body morphology could be linked to migratory strategy (residency/migration) within a species in **paper VI**. I caught residents (in lake Krankesjön) and migrants (in its connected streams) in November when spatial segregation of the two life-history forms was pronounced (as evidenced by our RFID-antenna system). In addition we caught roach from five closed lakes (i.e. with no opportunity for migration) and from three open lakes (i.e. with opportunity for migration). All specimens were photographed and I used a geometric morphometric approach (based on analysis of landmark coordinates) to explore variation in body morphology among and within our study populations.

RESULTS AND CONCLUSIONS

- When exposed to predatory pike, crucian carp showing risky behaviours (bold individuals) expressed a significantly greater morphological defence as compared to shy individuals. Furthermore, shy fish exhibited greater absolute behavioural plasticity (change in boldness) as compared to bold fish. Furthermore, I report links between animal personality and migratory behaviour with bolder individuals being more likely to undertake a winter migration as compared to shyer ones. Hence, I show that boldness, a key personality trait influences other ecologically significant processes such as migration and phenotypic plasticity (i.e. inducible defences). Furthermore, our results suggest that bold individuals engage in compensatory anti-predator strategies ('phenotypic compensation') to mediate some of the costs of being bold.

- One such cost can be increased susceptibility to predation and I report a predation cost to boldness: the individual boldness score of prey was positively related to susceptibility to avian predation. Assessing the costs and benefits of divergent behavioural strategies in the wild is critical if we are to gain insights into how behavioural diversity is maintained in natural populations.

- I show that that the decision to migrate or not can be influenced by changes to the predator environment. Roach that had experienced prior exposure to a live predator (i.e. an elevated perception of direct risk) demonstrated higher propensities for migration than fish originating from experimental environments absent of predators. This is important because of the potential ecological implications that changes in the predator community could have via indirect behavioural effects upon migratory animals.

- Variation in migratory timing differed seasonally with spring migrants showing less variance and a higher degree of migration synchrony as compared to autumn migrants. Here I also address the consequences of individual variation in migratory behaviour: survival was strongly linked with the timing of lake return migration but not to autumn lake departure timing. Hence individual variation in the timing of the migratory journey has powerful fitness implications.

- Our data suggests that migration is a compensatory behavioural strategy. Given that this compensatory strategy is energetically costly, we would predict that migratory individuals' morphology should reflect the challenges associated with the demands of the migratory lifestyle. I found that roach morphology was related to migratory life history as fish from open lakes (migration opportunity) and migratory individuals from lake Krankesjön had a more slender, hydrodynamic morphology as compared to specimens from closed lakes (no migration opportunity) and residents in lake Krankesjön. These results are consistent with hydrodynamic theory and suggest that a more fusiform morphology is beneficial for a migratory life-history strategy in this species.

In summary, my results highlight the powerful role that ecological forces, such as predation, can have in shaping patterns of individual variation in wild populations of animals, and, importantly, that these different behavioural strategies can have profound consequences for survival and thereby individual fitness. Individual variation in survival as a function of phenotype is the raw material upon which natural selection acts, and yet the ecological drivers of evolution remain poorly studied in wild populations. Working at the individual level in the wild poses significant challenges, but can provide rich insights into the mechanisms of the interplay between ecosystem dynamics and evolutionary processes.

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