The eco-evo-devo of stickleback personalities

Gismann, Jakob R.L.

DOI:
10.33612/diss.1165822955

Publication date:
2025

1

Introduction

"*All the birds and creatures of the world are unutterably themselves.*"

– David Whyte

Introduction

Animal behaviour has long been a topic of human curiosity. Detailed descriptions of animals' behaviours date back to Aristotle (e.g., in 'History of Animals') and probably well before that. Already infants exhibit a marked curiosity when confronted with animals. With little fear, they pick up ants or snails or try to catch lizards. They point out birds in the sky, mimic the sounds of cats and dogs and ask countless questions about their favourite animals (of which each child seems to have at least one, or, as in my case, many). It almost seems as if most humans are born naturalists. Studies of animal behaviour have been an important part of biology for a good century now, and their work in this field won Konrad Lorenz, Karl von Frisch and Nikolaas Tinbergen the Nobel Prize in Physiology or Medicine in 1973. The three Nobel laureates, and many ethologists after them, were mostly concerned with 'species-specific' behaviours. Yet, as every pet owner will attest, individual animals differ in behaviour from one another.

Already Charles Darwin emphasised the importance of (genetic and phenotypic) variation as providing the raw material for selection to act upon (Darwin, 1859). However, for a long time, individual behavioural variation was mostly considered as statistical 'noise' around a selected 'appropriate' or 'true' mean value (Wilson, 1998). Only in the past few decades have biologists systematically explored the causes and consequences of individual differences in behaviour (Bolnick et al., 2003; Réale et al., 2010; Sih et al., 2004; Wolf et al., 2007; Wilson, 1998). The realisation that individual behavioural differences are ubiquitous in the animal kingdom, that they persist independently of sex or other morphological characteristics, and are stable over time, ultimately led to the establishment of the field of 'animal personality' within behavioural biology.

In this thesis, I aim to study personality variation in three-spined sticklebacks (Gasterosteus aculeatus) from an integrative ecological, evolutionary and developmental perspective. My PhD project is the outcome of the grant 'The Eco-Evo-Devo of Social Personalities' that was awarded by the Dutch Research Council (NWO) to my PhD advisers. In this introduction, I will explain what animal personalities entail in the eyes of behavioural ecologists and how I define social personalities. Then, I will provide reasons why personality studies are worthwhile and what an 'Eco-Evo-Devo' approach to animal personality implies. I then motivate the choice of our study species and experimental methodology and conclude with a brief introduction of the thesis chapters.

Animal Personality and Social Personalities

Of the many definitions of animal personality, I consider the following the most useful because it entails most scientists' ideas about this concept: The term animal personality describes between-individual differences in behavioural tendencies that are consistent over time and across contexts (Dall et al., 2004; Stamps and Groothuis, 2010a). This definition contains the hallmarks of animal personality, namely that individuals behave differently from one another, that there is temporal consistency, and that there is contextual consistency in behavioural expression (Kaiser and Müller, 2021).

In its most basic interpretation, the term animal personality indicates that behaviours differ between individuals and that individual behaviour is repeatable (in a statistical sense). Yet, in a stricter sense, what is meant when talking about animal personality is that there is structure and organisation to animals' behaviours. I thus purposefully used the term 'behavioural tendency' (rather than 'behaviour') in the definition above, because it better signifies this underlying organisation. When describing animals' behaviours, rather than describing the behaviour itself (for example, biting a conspecific), scientists typically use terms describing behavioural tendencies such as boldness or aggression (also called personality traits). These tendencies cannot be measured directly; instead, they are assessed through observations of measurable behaviours. To describe an individual's boldness, scientists may, for example, study behaviours such as the time spent outside of cover when an individual is placed in a novel environment or how often an individual approaches a predator. Behavioural tendencies thus describe that there are underlying behavioural patterns or dispositions which govern animals' behaviour in specific situations (Kaiser and Müller, 2021).

Speaking of behavioural tendencies also helps to understand what is meant by contextual consistency. Contextual consistency typically refers to situations where animals consistently differ in behaviour across different ecological contexts (e.g., under low and high temperatures). Yet, for some (e.g., Stamps and Groothuis, 2010a; Wolf and Weissing, 2012), contextual consistency also refers to behavioural tendencies expressed in functionally different contexts, such as aggression toward conspecifics when fighting for territories and aggression in an anti-predator context. Observations of such contextual consistency led to the introduction of the term ‘behavioural syndrome’, which generally describes any suites of correlated behaviours in a population (Sih et al., 2004). Depending on one’s interpretation, contextual consistency can thus encompass the concept of behavioural syndromes. The most well-known behavioural syndrome is the ‘aggressiveness-boldness’ syndrome. It was famously described by Huntingford (1976) in a population of three-spined sticklebacks (Gasterosteus aculeatus), where territorial aggression and boldness toward a predator were positively correlated. The aggressiveness-boldness syndrome and many other behavioural syndromes have since been described in countless other species. Individuals within a population can then be classified by their behavioural type, depending on the behavioural combination they display.

While temporal consistency is easily intuited, meaning behavioural differences are stable over time, there is little consensus about the timeframes. Depending on the research question, these can span from minutes (e.g., behaviour before and after exposure to a predator) to years (e.g., how juvenile behaviour relates to adult behaviour). The term behavioural tendency also better captures the fact that behaviour is plastic. Despite consistency across time and context, individuals’ behaviours can change. While the level of measurement is on the individual, animal personality research focuses on individuals’ behaviours relative to one another (Stamps and Groothuis, 2010b). Consistency in animal personality research thus describes that an individual’s score of a particular behaviour, for example, remains consistently higher than others’ when testing at a later time point or across different contexts.

As for most animals, conspecific interactions are crucial to many aspects of their life, social behaviour is an integral part of animal personality studies. Being social can come with many benefits, such as increased protection from predators (Magurran and Pitcher, 1987; Treherne and Foster, 1982) or information about resource abundance (Dall et al., 2005), but it can also inflict costs, such as increased physiological stress (Creel et al., 2013) or increased risk of pathogen transmission (Albery et al., 2021). Nevertheless, the consequences of variation in social behaviour for ecological and evolutionary processes have received much less attention than many other behaviours (Gartland et al., 2022).

The term “social personality” can be understood from two perspectives. From a personality trait perspective, it explores how social individuals are toward their conspecifics. Such sociability (or sociality) is typically defined as an individual's tendency to associate with conspecifics for reasons that are not related to reproduction (or aggression) (Gartland et al., 2022). Consistent individual variation in sociability has been demonstrated in many species across many taxa and can co-vary with other behavioural traits to form behavioural syndromes (Gartland et al., 2022; Réale et al., 2010). Individuals differing in sociability have for example been shown to prefer different social habitats and to differ in dispersal decisions (Cote and Clobert, 2007). While sociability presents an important aspect for research on social personalities, these go beyond the narrow definition of sociability as formulated in the sense of 'prosocial' behaviour. Social personalities for me encompass all interactions between conspecifics, and thus, for example, also individuals' aggressiveness or competitive behaviour during breeding.

Therefore, when describing social personalities, one also has to ask to what extent an individual's behaviour is affected by its social environment. From this responsiveness perspective, one can ask whether and how an individual's behaviour changes following interactions with conspecifics. Many behaviours, such as boldness (Jolles et al., 2016; Webster et al., 2007), exploration (Ward, 2012), activity (Fürtbauer and Fry, 2018), or foraging behaviour (Dyer et al., 2009; Michelena et al., 2009), can be affected by the social context and the behaviour of the interacting partners (e.g., social conformity, social facilitation; reviewed in Webster and Ward, 2011). When considering the social environment, individuals' phenotypes, because they partially depend on the phenotype of their interacting partners, can thus be described as 'interactive phenotypes' (Dingemanse and Araya-Ajoy, 2015). Similar to other environmental factors, social environments during ontogeny, such as the number of conspecifics or the presence of parents, can have long-lasting effects on an individual's behaviour later in life (Abbey-Lee et al., 2018; Fischer et al., 2015; Kozak and Boughman, 2012).

Although definitions and terms in animal personality research are often still vague and open to interpretation, in practice, scientists performing animal personality studies agree on common methodologies. Firstly, by necessity, the object of study is the individual. Individuals are then tested for their behaviour not only once but repeatedly, often across different ecological contexts. Furthermore, studies typically assess the expression of several behaviours. Researchers then typically ask how behaviours relate to each other and how they relate to other characteristics of the individual. If conducted this way, animal personality studies allow to assess how behaviour is organised, how individuals relate to one another in their behaviour and how behavioural variation relates to other environmental or life-history characteristics.

Ultimately, this shared way of observing and testing animals' behaviour lies at the heart of animal personality research.

Why Study Individual Behavioural Differences?

Individual behavioural differences within populations are ubiquitous and can have significant implications for ecology and evolution (reviewed in Wolf and Weissing (2012) and see Mittelbach et al. (2014) for ecological consequences in fish specifically). To a large extent, behaviour mediates how individuals interact with their environment. Individuals differing in, for example, migration or dispersal tendencies, movement behaviour, or social behaviours will likely differ in the environments they experience. As a result, selection pressures may vary between individuals, and personality differences regularly result in differential survival and/or reproductive success (Biro and Stamps, 2008; Dingemanse et al., 2004; Nicolaus et al., 2012; Sabol et al., 2020; Smith and Blumstein, 2008).

Moreover, when environments change, individuals typically first react behaviourally (Wong and Candolin, 2015), such that understanding how organisms can persist in ever faster-changing environments ('HIREC'; Sih, 2013) requires an understanding of individuals' behaviour. The study of individual behavioural differences thus promises to foster our understanding of ecological processes such as population dynamics and demography, spatial distributions, or dispersal, which can, in turn, affect evolutionary processes (Shaw, 2020; Wolf and Weissing, 2012). The recognition that personality differences are often linked to differences in fitness prompted a surge in animal personality studies, integrating questions about the maintenance and evolution of individual differences in behaviour (Dingemanse and Réale, 2005; Wolf and Weissing, 2010).

I want to briefly cite some passages from Nikolaas Tinbergen's famous essay 'On Aims and Methods of Ethology' (1963) because it helps illustrate the methods used to study individual behavioural differences today. Tinbergen describes both the importance and the difficulties of testing the 'survival value', or, in other words, the adaptiveness of an animal's behaviour. He states: "The method to demonstrate survival value of any attribute of an animal is to try whether or not the animal would be worse off if deprived of this attribute". He argues that this method may be successful for the physical structures of an animal, whereas it is much harder regarding an animal's behaviour. He continues: "But how does one make an experimental animal which lacks just one behaviour pattern and is otherwise normal?". Tinbergen's answer to these difficulties more than 60 years ago was the comparative study of species-specific behaviours. Today, following the realisation in Ethology of the existence of stable individual-specific behaviours, or animal personalities, we make use of that individual behavioural variation by providing us with precisely the experimental animals that Tinbergen described as needed to study the survival value of animal behaviour.

On the Origins of Individuality

Where does behavioural individuality come from? This long-standing question, as played out in the 'nature vs. nurture' debate, is today commonly answered by partly resulting from variation in an organism's genes and partly from environmental effects acting on the organism. Here, it is important to recognise that the answer "It's both nature and nurture" not only indicates that both factors act on top of each other. The crucial point is that an intricate interplay exists between an organism's genes and its environment. Phenotypic differences derive not only from genetic and environmental influences but from genes in interaction with the environment. Because genes and the environment do not act independently from one another, the answer 'it is both nature and nurture' could thus better be described as 'it is the interaction of nature with nurture'. What links the two, is the process of development. Each individual carries a unique genetic makeup which predisposes their phenotype toward certain outcomes, which the environment and individual experiences shape further. Feedback loops (positive and negative) between genes and the environment can drastically enhance (or decrease) the effects of each factor. Behavioural ecologists are, of course, aware of the role that development plays in shaping an individual's behaviour (see 'developmental reaction norms', Stamps and Groothuis, 2010b). Still, I believe that the importance of development as a source of variation in individuality is often underappreciated. Particularly, the role of stochasticity (or randomness) during development needs more attention as a source of variation in individuality.

Some recent experiments on the Amazon molly (*Peocilia formosa*) provided intriguing examples of individual differences in behaviour in the (near) absence of genetic and environmental variation in a vertebrate system. Amazon mollies are naturally clonal fish that do not require parental care. Bierbach et al. (2017) and Laskowski et al. (2022a) found individual differences in behaviour even in genetically identical individuals housed individually in near-identical environments from birth. Importantly, behavioural individuality was observed from the first day of life, indicating that factors predating birth were instrumental in shaping individuality (Laskowski et al., 2022a). These findings suggest that developmental stochasticity is an important contributor to the observed behavioural variation and should be considered a third key factor, next to genetic and environmental influences, contributing to behavioural variation.

More evidence comes from the field of neuroscience, where the importance of stochasticity, or randomness in developmental processes, has been appreciated for much longer (Oates, 2011). Using *Drosophila melanogaster*, Linneweber et al. (2020) have, for example, shown that individuality in object-orientation behaviour directly resulted from random variability in early developmental neuron wiring asymmetry –an intrinsically stochastic process– in the *Drosophila* dorsal cluster neurons. The flies' object orientation behaviour was stable over several days and weeks. The study demonstrates how random developmental processes occurring during early brain development can shape complex behaviours. A larger appreciation and more investigations into the occurrence and strength of such stochastic developmental factors in contributing to behavioural individuality would help to answer questions on the causes of individuality in animals and humans and may ultimately lead to the realisation that diversity in phenotypes is, in part, an inevitable outcome of the organism's complex developmental process.

Notably, such stochastic individuality may be an adaptive feature in itself and not simply an unavoidable outcome of development (Honegger and de Bivort, 2017). For example, several studies suggest that both single behaviours and suites of correlated behaviours (i.e., behavioural syndromes) can derive from such developmental stochasticity (Laskowski et al., 2022b; Vogt et al., 2008). Furthermore, the level of stochastic variability observed within a genotype (intra-genotypic variability) can be heritable and vary across genotypes (Ayroles et al., 2015; Stamps et al., 2013). Theory long suggested that such 'mixed' strategies from a game-theoretical perspective, as well as diversifying bet-hedging strategies resulting from such intra-genotypic variability, can be adaptive (Wolf et al., 2011). The interconnectedness of ecological, developmental and evolutionary processes in shaping individual variation in behaviour, as described above, thus calls for the study of animal personality from all these perspectives.

An Eco-Evo-Devo Approach to Animal Personality

Ten years prior to winning the Nobel Prize, Nikolaas Tinbergen formulated his own four famous questions about animals' behaviour, describing the central aims and problems in the biological study of behaviour (ethology) (Tinbergen, 1963). His four questions call for studying animal behaviour by asking about the survival value of behaviour and how it evolved (evolution), the physiological causes and ontogeny of behaviour (development), and the interplay between behaviour and the environment (ecology). His proposed approach shapes the field of behavioural ecology still today. The previously discussed effects of developmental stochasticity and the fact that environments can shape behaviour demonstrate the importance of incorporating developmental and ecological perspectives into animal personality studies. Furthermore, as individual differences in behaviour can result in differences in reproductive success and survival, one must consider how selection of phenotypes shapes behaviours in a given environment. As these processes are intricately linked, this thesis aims to study social personalities from an integrative eco-evo-devo perspective. As evolutionary processes cannot be studied empirically in sticklebacks during the timeframe of a PhD thesis, we had originally intended to complement the empirical work on questions of developmental and ecological effects with theoretical evolutionary models. While I co-authored two such individual-based model studies during my PhD, I did not perform any modelling myself and have thus not incorporated these studies into this thesis. In the first theoretical study (Netz et al., 2022), we critically discuss how the link between animal personalities and the spatial distribution of foragers is implemented in a recent model on this topic. We show that modelling details have a considerable impact on the evolutionary predictions to be drawn and we propose a more consistent modelling approach. In the second study (Gupte et al., 2023), we considered a model for the evolution of movement strategies that led to the emergence of (social) personalities: in the model, some individuals based their movement decisions much more on social information than other individuals. Our study further demonstrates that a change in the environment (here, the introduction of a novel pathogen that makes social interactions more costly due to increased risk of infection) can induce the surprisingly rapid evolution of alternative social movement strategies, which in the scenario considered led to social distancing.

Although my thesis does not include an evolutionary modelling study, it still addresses questions regarding the evolution of animal personalities. For example, in Chapter 4, I report on a breeding experiment that allowed me to quantify the mating success of males and relate it to their personalities. This provides some first insights into the fitness implications of personality differences.

The stickleback model system

Three-spined sticklebacks (*Gasterosteus aculeatus*) are an ideal model for studying animal personality in an eco-evo-devo approach. Sticklebacks are small fish –typically measuring between 4 and 10cm– that inhabit marine as well as freshwater environments across Asia, North America, and Europe. They are short-lived (typically living only 1-2 years) but recorded to live up to 8 years in a Canadian population (Reimchen, 1992). Stickleback populations display remarkable variation not only in life history but also in morphology and behaviour. There is a long tradition among biologists to study sticklebacks, and for more than 50 years they are a model system for behavioural, ecological and evolutionary studies (Hendry et al., 2013; Huntingford and Ruiz-Gomez, 2009; McKinnon and Rundle, 2002; Norton and Gutiérrez, 2019). Sticklebacks were also instrumental in early studies in the field of animal personality. By studying stickleback populations differing in predation pressure, researchers demonstrated the occurrence of a behavioural syndrome (aggressiveness-boldness), but only in populations under threat of predation (Bell, 2005; Dingemanse et al., 2007). These studies led to the realisation that syndromes are not just a byproduct of physiological processes but strongly reflect environmental conditions. Furthermore, these studies raised the follow-up question at what point during an individual's development environmental conditions have the most pronounced effect, prompting inquiries about the ontogeny of animal personality. For our purposes, sticklebacks were particularly useful for several additional reasons: Sticklebacks are native to the Netherlands and easy to keep in the laboratory as well as in experimental mesocosms. This was crucial for the behavioural experiments presented in this thesis. Furthermore, in the Netherlands, water management efforts over the past decades have permanently cut off several populations from their ancestral migratory populations. These isolated populations are now permanently restricted to freshwater environments, creating a sort of 'natural experiment'.

Ramesh et al. (2022) found that about 60 years of isolation led to changes in morphology as well as behaviour and that genetic differentiation at least partially underlies these differences (Ramesh et al., 2021). We made use of this behavioural variation in Chapters 2 and 3 of this thesis, investigating differences in movement behaviours across spatial scales and the effects of social group composition on movement. The stickleback mating system additionally allowed me to quantify the link between personality and reproductive success. Male sticklebacks build nests during the breeding season, which allowed us to design experiments that included observations of reproductive behaviours and the monitoring of males' success in establishing territories and acquiring eggs (Chapter 4). Lastly, sticklebacks do not live in rigid social groups but regularly move between shoals that repeatedly break up and re-form (Ward et al., 2002). The dynamic nature of the stickleback social system thus makes them a suited system for studies on the active choice of the social environment. This area of study is rarely explored in sufficient detail in fish. Chapter 5 of this thesis presents our attempt to investigate this topic.

The Mesocosm

To employ this integrative eco-evo-devo approach in practice, we felt the need to design a new experimental setup. When not testing behaviours in the wild –which is especially challenging for aquatic animals– the most widely used approach to study behaviour on the individual level is to place subjects in highly controlled and standardised laboratory arenas. While this approach has undoubtedly proven fruitful and will continue to do so in the future, it did not seem appropriate for our planned experiments. We thus decided to study behaviours in a two-fold approach: 1) using classical laboratory setups as described above and 2) using an experimental mesocosm system, which was fundamentally important for this thesis. The mesocosm consists of several connectable (above-ground) ponds placed outside under a tarp net. Each pond is 1.6m in diameter, has four potential connections to other ponds, and contains up to 1200L of water. Individual ponds can be connected via opaque tubes 11 cm in diameter and 1.5 m long. The water for the mesocosm is directly pumped from a water body typical for stickleback habitats in the Netherlands next to the system. To monitor the fish's behaviour in the mesocosm, we implanted each fish with a PIT tag ('Passive Integrative Transponder') that carries a unique code which can be detected with the help of RFID ('Radio-frequency Identification') antennas. To record individuals' movement between ponds, we fitted circular antennas to both ends of the connecting tubes, which allowed us to detect movement through the tubes and the direction of movement. This way, we can continuously monitor each individual's current position and all its movements in the mesocosm in large groups of fish for several weeks. This experimental approach starkly contrasts laboratory tests, typically performed on isolated individuals and often lasting only a few minutes. Surprisingly few studies have investigated to what extent behaviour measured under such controlled laboratory conditions translates to behaviour in the wild. For example, Krause et al. (2000) found that some factors which affected association preferences in the lab could not be demonstrated to do so in the wild. Similar results have been found for startle responses in sea anemones, where the mean startle duration differed between the lab and the field (Osborn and Briffa, 2017).

Furthermore, variations in factors such as temperature or turbidity in the wild are often highly variable. They have been shown to affect a range of behaviours in fish (Michael et al., 2021; Zanghi et al., 2023) but are typically held constant or eliminated in the lab. While some studies found that observations in the field match observations from the lab (Klaminder et al., 2016; Ward et al., 2017), their relationship is rarely tested explicitly. To rely on the assumption that behaviour measured in the laboratory is representative of behaviour under natural conditions seemed inappropriate for our purposes. The fact that we can observe large groups of freely moving fish in the mesocosm was especially crucial for this thesis. To study social personalities as we had set out, we needed setups that could be experimentally manipulated and in which fish could freely interact with each other, enabling them to exhibit a wide range of social behaviours.

In our mesocosm, fish can consequently choose to join a social group, leave one group and instead join another, associate with a specific individual, or choose to stay alone. We thus believe that results obtained in the mesocosms have higher ecological validity than those from most classical laboratory studies, especially regarding social behaviour. While recent technical advances allow for more detailed observations of social behaviour, even in the wild (King et al., 2018), in aquatic environments, detailed individual-level observations at scale remain a challenge. The environment in the mesocosm resembles the conditions that fish experience in the wild much closer regarding, for example, spatial scales, the abiotic environment (water, light, temperature), and, as already mentioned, the social environment, than possible in the lab and might thus provide a bridge between highly controlled laboratory studies and challenging studies in the wild. Furthermore, we used the mesocosm to manipulate environmental conditions during ontogeny, such that fish grew up under the impression of predators in their habitat and developed in social groups of different sizes.

Brief Outline of this Thesis

In this thesis, I report on four experiments investigating various aspects of animal personalities (Figure 1.1). In Chapter 2, we investigate animal personality from an evolutionary perspective, while Chapters 3 and 4 represent studies from an ecological perspective. In Chapter 5, we investigate developmental processes and their link to animal personality. Furthermore, I included two 'intermezzos' conducted mainly by students under my supervision. These proved valuable pilot studies for my larger experiments and were interesting in their own right. The modularity of the mesocosm system allowed us to create experimental setups specifically designed for the research questions at hand, such that all experiments – except for those in Chapters 2 and 3– were carried out in different mesocosm conformations.

In **Chapter 2**, we asked whether about 60 generations of isolation resulted in behavioural differentiation between two populations of wild sticklebacks. In the Netherlands, water-management efforts have permanently isolated stickleback populations into freshwater habitats so that these can no longer migrate to the sea. Specifically, we tested whether these 'land-locked' resident populations that had been cut off from access to the sea about 60 years ago differ from migratory populations in large-scale 'migration-like' movement behaviours.

In **Chapter 3**, building on our findings from Chapter 2, we investigate how animals' social environments can shape individuals' behaviour. As social group cohesion can have many benefits, individuals may need to adopt the behaviour of their social group. In fish, most experiments of that nature substantially limit individuals' social options. To test these processes in freely interacting fish and under semi-natural conditions, we studied if individuals' movement behaviour in the mesocosm changed based on the composition of their social group.

In **Chapter 4**, I investigate how personality variation can impact ecological processes and have potential implications for fitness ('eco-evo'). I examined how individual behavioural differences affect dispersal decisions and settlement success in a novel environment. Groups of fish of known phenotypes from both sexes were released in a mesocosm setup containing limited breeding opportunities. We then monitored variation in dispersal behaviour (departure, transience and settlement) and male-mating success and assessed their relationship to fish personality.

In the **Intermezzo**, we investigate how early-life environments can affect social behaviour, which helped to inform the experiment presented in Chapter 5. To this end, we raised young sticklebacks under different environmental conditions, manipulating social group size and perceived predation. After about a year-long manipulation, before the onset of the breeding season, we tested whether ontogenetic environments affect sociality.

Chapter 5 addresses the effects of the ontogenetic environment on social behaviour and spatial distributions in adult fish during breeding ('devo-eco'). Using the same fish as Intermezzo 2, we released large groups of fish into a mesocosm setup large enough to allow for spatial structuring of phenotypes. I then assessed behaviour, association patterns, and spatial distributions in regard to the fish's ontogenetic experience.

I conclude the thesis with some **Afterthoughts**.

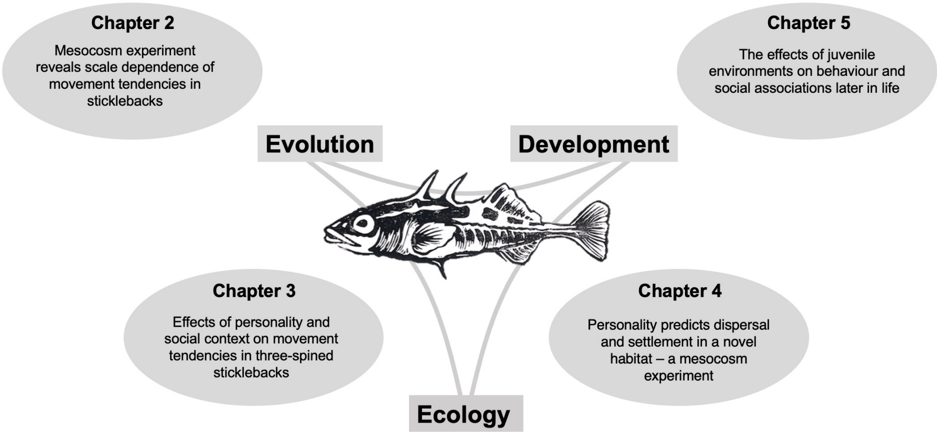

Figure 1.1 | Schematic overview of the thesis data chapters.

References

Abbey-Lee, R. N., Uhrig, E. J., Zidar, J., Favati, A., Almberg, J., Dahlbom, J., Winberg, S., and Løvlie, H. (2018). The influence of rearing on behavior, brain monoamines, and gene expression in three-spined sticklebacks. *Brain, Behavior and Evolution*, 91:201–213.

Albery, G. F., Kirkpatrick, L., Firth, J. A., and Bansal, S. (2021). Unifying spatial and social network analysis in disease ecology. *Journal of Animal Ecology*, 90:45–61.

Ayroles, J. F., Buchanan, S. M., O'Leary, C., Skutt-Kakaria, K., Grenier, J. K., Clark, A. G., Hartl, D. L., and Bivort, B. L. D. (2015). Behavioral idiosyncrasy reveals genetic control of phenotypic variability. *Proceedings of the National Academy of Sciences of the United States of America*, 112:6706–6711.

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

Bierbach, D., Laskowski, K. L., and Wolf, M. (2017). Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nature Communications*, 8:1–7.

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

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161:1–28.

Cote, J. and Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, 274:383–390.

Creel, S., Dantzer, B., Goymann, W., and Rubenstein, D. R. (2013). The ecology of stress: effects of the social environment. *Functional ecology*, 27(1):66–80.

Dall, S. R., Giraldeau, L. A., Olsson, O., McNamara, J. M., and Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution*, 20:187–193.

Dall, S. R. X., Houston, A. I., and McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7:734–739.

Darwin, C. (1859). On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life. (J. Murray).

Dingemanse, N. J. and Araya-Ajoy, Y. G. (2015). Interacting personalities: Behavioural ecology meets quantitative genetics. *Trends in Ecology and Evolution*, 30:88–97.

Dingemanse, N. J., Both, C., Drent, P. J., and Tinbergen, J. M. (2004). Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1541):847–852.

Dingemanse, N. J. and Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142:1159–1184.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., and Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *The Journal of animal ecology*, 76:1128–38.

Dyer, J. R. G., Croft, D. P., Morrell, L. J., and Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20:165–171.

Fischer, S., Bessert-Nettelbeck, M., Kotrschal, A., and Taborsky, B. (2015). Rearing-group size determines social competence and brain structure in a cooperatively breeding cichlid. *American Naturalist*, 186:123–140.

Fürtbauer, I. and Fry, A. (2018). Social conformity in solitary crabs, carcinus maenas, is driven by individual differences in behavioural plasticity. *Animal Behaviour*, 135:131–137.

Gartland, L. A., Firth, J. A., Laskowski, K. L., Jeanson, R., and Ioannou, C. C. (2022). Sociability as a personality trait in animals: methods, causes and consequences. *Biological Reviews*, 97(2):802–816.

Gupte, P. R., Albery, G. F., Gismann, J., Sweeny, A., and Weissing, F. J. (2023). Novel pathogen introduction triggers rapid evolution in animal social movement strategies. *Elife*, 12:e81805.

Hendry, A. P., Peichel, C. L., Matthews, B., Boughman, J. W., and Nosil, P. (2013). Stickleback research: The now and the next. *Evolutionary Ecology Research*, 15:111–141.

Honegger, K. and de Bivort, B. (2017). Stochasticity, individuality and behavior. *Current Biology*, 28:R8–R12.

Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback , gasterosteus aculeatus reproductive tests : Aggression within the. *Animal Behavior*, 24:245–260.

Huntingford, F. A. and Ruiz-Gomez, M. L. (2009). Three-spined sticklebacks gasterosteus aculeatus as a model for exploring behavioural biology. *Journal of Fish Biology*, 75:1943–1976.

Jolles, J. W., Taylor, B. A., and Manica, A. (2016). Recent social conditions affect boldness repeatability in individual sticklebacks. *Animal Behaviour*, 112:139–145.

Kaiser, M. I. and Müller, C. (2021). What is an animal personality? *Biology and Philosophy*, 36:1–25.

King, A. J., Fehlmann, G., Biro, D., Ward, A. J., and Fürtbauer, I. (2018). Re-wilding collective behaviour: An ecological perspective. *Trends in Ecology Evolution*, 33:347–357.

Klaminder, J., Hellström, G., Fahlman, J., Jonsson, M., Fick, J., Lagesson, A., Bergman, E., and Brodin, T. (2016). Drug-induced behavioral changes: Using laboratory observations to predict field observations. *Frontiers in Environmental Science*, 4:81.

Kozak, G. M. and Boughman, J. W. (2012). Plastic responses to parents and predators lead to divergent shoaling behaviour in sticklebacks. *Journal of Evolutionary Biology*, 25:759–769.

Krause, J., Butlin, R. K., Peuhkuri, N., and Pritchard, V. L. (2000). The social organization of fish shoals: a test of the predictive power of laboratory experiments for the field. *Biological Reviews*, 75:477–501.

Laskowski, K. L., Bierbach, D., Jolles, J. W., Doran, C., and Wolf, M. (2022a). The emergence and development of behavioral individuality in clonal fish. *Nature Communications*, 13:6419.

Laskowski, K. L., Chang, C.-C., Sheehy, K., and Aguiñaga, J. (2022b). Consistent individual behavioral variation: what do we know and where are we going? *Annual Review of Ecology, Evolution, and Systematics*, 53(1):161–182.

Linneweber, G. A., Andriatsilavo, M., Dutta, S. B., Bengochea, M., Hellbruegge, L., Liu, G., Ejsmont, R. K., Straw, A. D., Wernet, M., Hiesinger, P. R., and Hassan, B. A. (2020). A neurodevelopmental origin of behavioral individuality in the drosophila visual system. *Science*, 367:1112–1119.

Magurran, A. E. and Pitcher, T. J. (1987). Provenance, shoal size and the sociobiology of predator-evasion behaviour in minnow shoals. *Proceedings of the Royal Society of London - Biological Sciences*, 229:439–465.

McKinnon, J. S. and Rundle, H. D. (2002). Speciation in nature: The threespine stickleback model systems. *Trends in Ecology and Evolution*, 17:480–488.

Michael, S. C. J., Patman, J., and Lutnesky, M. M. F. (2021). Water clarity affects collective behavior in two cyprinid fishes. *Behavioral Ecology and Sociobiology*, 75:120.

Michelena, P., Sibbald, A. M., Erhard, H. W., and McLeod, J. E. (2009). Effects of group size and personality on social foraging: The distribution of sheep across patches. *Behavioral Ecology*, 20:145–152.

Mittelbach, G. G., Ballew, N. G., and Kjelvik, M. K. (2014). Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, 71:927–944.

Netz, C., Ramesh, A., Gismann, J., Gupte, P. R., and Weissing, F. J. (2022). Details matter when modelling the effects of animal personality on the spatial distribution of foragers. *Proceedings of the Royal Society B*, 289(1970):20210903.

Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P. M., Ubels, R., Both, C., Kempenaers, B., and Dingemanse, N. J. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, 279:4885–4892.

Norton, W. H. and Gutiérrez, H. C. (2019). The three-spined stickleback as a model for behavioural neuroscience. *PLoS ONE*, 14:1–18.

Oates, A. C. (2011). What's all the noise about developmental stochasticity? *Development*, 138:601–607.

Osborn, A. and Briffa, M. (2017). Does repeatable behaviour in the laboratory represent behaviour under natural conditions? a formal comparison in sea anemones. *Animal Behaviour*, 123:197–206.

Ramesh, A., Domingues, M. M., Stamhuis, E. J., Groothuis, T. G. G., Weissing, F. J., and Nicolaus, M. (2021). Does genetic differentiation underlie behavioral divergence in response to migration barriers in sticklebacks? a common garden experiment. *Behavioral Ecology and Sociobiology*, 75:161.

Ramesh, A., Groothuis, T. G. G., Weissing, F. J., and Nicolaus, M. (2022). Habitat fragmentation induces rapid divergence of migratory and isolated sticklebacks. *Behavioral Ecology*, 33:167–177.

Reimchen, T. E. (1992). Extended longevity in a large-bodied stickleback, gasterosteus, population. *Canadian field-naturalist. Ottawa ON*, 106(1):122–125.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., and Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365:4051–4063.

Sabol, A. C., Lambert, C. T., Keane, B., Solomon, N. G., and Dantzer, B. (2020). How does individual variation in sociality influence fitness in prairie voles? *Animal Behaviour*, 163:39–49.

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement ecology*, 8(1):12.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, 85:1077–1088.

Sih, A., Bell, A., and Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in ecology & evolution*, 19(7):372–378.

Smith, B. R. and Blumstein, D. T. (2008). Fitness consequences of personality: A meta-analysis. *Behavioral Ecology*, 19:448–455.

Stamps, J. and Groothuis, T. G. G. (2010a). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85:301–325.

Stamps, J. A. and Groothuis, T. G. G. (2010b). Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365:4029–4041.

Stamps, J. A., Saltz, J. B., and Krishnan, V. V. (2013). Genotypic differences in behavioural entropy: unpredictable genotypes are composed of unpredictable individuals. *Animal behaviour*, 86:641.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20:410–433.

Treherne, J. and Foster, W. (1982). Group size and anti-predator strategies in a marine insect. *Animal Behaviour*, 30:536–542.

Vogt, G., Huber, M., Thiemann, M., Boogaart, G. V. D., Schmitz, O. J., and Schubart, C. D. (2008). Production of different phenotypes from the same genotype in the same environment by developmental variation. *The Journal of experimental biology*, 211:510–523.

Ward, A. J. (2012). Social facilitation of exploration in mosquitofish (gambusia holbrooki). *Behavioral Ecology and Sociobiology*, 66:223–230.

Ward, A. J., Botham, M. S., Hoare, D. J., James, R., Broom, M., Godin, J. G. J., and Krause, J. (2002). Association patterns and shoal fidelity in the three-spined stickleback. *Proceedings of the Royal Society B: Biological Sciences*, 269:2451–2455.

Ward, A. J. W., Schaerf, T. M., Herbert-Read, J. E., Morrell, L., Sumpter, D. J. T., and Webster, M. M. (2017). Local interactions and global properties of wild, free-ranging stickleback shoals. *Royal Society Open Science*, 4:170043.

Webster, M. M., Ward, A. J. W., and Hart, P. J. B. (2007). Boldness is influenced by social context in threespine sticklebacks (gasterosteus aculeatus). *Behaviour*, 144:351–371.

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 353:199–205.

Wolf, M., Doorn, G. S. V., Leimar, O., and Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447:581–584.

Wolf, M., Doorn, G. S. V., and Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278:440–448.

Wolf, M. and Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365:3959–3968.

Wolf, M. and Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27:452–461.

Wong, B. B. M. and Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, 26:665–673.

Zanghi, C., Munro, M., and Ioannou, C. C. (2023). Temperature and turbidity interact synergistically to alter anti-predator behaviour in the trinidadian guppy. *Proceedings of the Royal Society B: Biological Sciences*, 290.