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The eco-evo-devo of stickleback personalities

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Afterthoughts

"So as to describe my walking, you must describe the space in which you find me."

– Alan Watts

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For the final chapter of this thesis, I would like to, for the most part, discuss some of the personal insights that I have gained studying animals' behaviour. Most people would agree, that obtaining a PhD is as much, if not more, a project of personal endeavour as one of scientific inquiry, and I thus believe this more private approach to my final chapter is warranted. I purposefully wrote that I study animals' behaviour rather than animal behaviour or animal personality. While this distinction is admittedly pedantic, it illustrates why I chose to become a behavioural ecologist. The terms animal behaviour and animal personality describe disciplines in biology relating to broader biological phenomena. When I say that I study animals' behaviour, I hope to convey that my motivation in pursuing this work is grounded in a deep fascination and curiosity about simply observing animals, ideally in their natural habitat. To me, observing and describing an idiosyncratic behaviour occurring only in a single species –or even in an individual– is fascinating and worthwhile, even without any larger biological implications. This does not mean that I do not find the bigger picture interesting. I too, often ponder potential explanations for a specific observation, but my starting point lies elsewhere. Instead of studying animal behaviour for its implications on ecological or evolutionary processes, I want to study animals' behaviour simply because I enjoy watching them 'do their thing'.

Unfortunately for me and anyone wanting to study behaviour, animals in the wild are often elusive. They often inhabit environments where direct observations are difficult or even impossible. Three-spined sticklebacks, the study species of this PhD, are among them. Sticklebacks are small fish which inhabit a wide range of habitats, from the open ocean to landlocked ditches. Individuals from migratory populations may swim vast distances to reach their breeding habitats in a river, while others permanently inhabit brackish estuaries or small freshwater lakes and rivers. Each of these environments presents their own challenges for behavioural observations, such as turbid conditions, deep water, or little accessibility. There may be brief periods or specific locations to catch a glimpse of sticklebacks' behaviour in the wild, but for most of their lives fish remain hidden from our eyes. These issues are not exclusive to fish or aquatic organisms; similar complications persist for many animals.

Two main methodological approaches address the challenges of obtaining detailed behavioural observations at scale. The first is observing individuals in the wild, often with the help of technological devices such as cameras, GPS or acoustic trackers, or accelerometers. The second, and most commonly used approach, is removing the animal from its natural environment and observing it under laboratory conditions. Both approaches are widely applied in behavioural ecology and have their respective strengths and weaknesses. For my PhD, we set out to study animal personalities in three-spined sticklebacks using a 'holistic' approach, explicitly recognizing that an animal's behaviour can not be understood without consideration of its past (evo-devo) and present (eco-devo) environments. These considerations made apparent that both classical approaches for behavioural studies alone were inadequate for our purposes. Field studies in our system did not allow for experimental manipulation of environments or collection of large-scale individual-level data. In contrast, laboratory approaches where individuals are often studied in isolation and/or on small temporal and spatial scales seemed sub-optimal, especially when studying social aspects of personalities. The mesocosm system that I developed during my PhD, represents an important step in the attempt to reap the benefits of both methodological approaches. Importantly, as I will elaborate on this later, I think that our approach not only differs in research methodology but also conceptually from many of the most widely used approaches in behavioural biology.

LESSONS LEARNED

In the following passages, I will elaborate on the 'lessons learned' from my experiments in the mesocosms. While most of these lessons are not necessarily novel and have been discussed in various places elsewhere, these are close to my heart. By illuminating these insights with specific examples from my research, I hope they can guide students starting animal personality research, and stimulate established behavioural biologists to reconsider the methods used.

The first big lesson learned from my PhD is that **testing environments matter**. Most laboratory tests are designed to yield easily quantifiable and repeatable behavioural data. Such standardized tests allow comparisons between individuals from the same population, from different populations or even across species and have thus proven to be invaluable tools for behavioural biologists. Yet, these same behavioural tests may present rather different challenges to an organism, depending on slight variations in the behavioural setup. Consequently, scientists may measure different behaviours. The realization that differences in methodology matter is not new (Walsh and Cummins, 1976),

and has helped in the establishment of standardized behavioural lab tests. Yet, I believe that behavioural biologists (including myself) have to be more careful in employing these tests. Open-field tests for example –maybe the most widely used behavioural tests in all of behavioural biology– have been described to measure a wide range of behavioural tendencies such as activity, exploration, neophobia, fear, or boldness. Often it is only small methodological differences, such as whether animals enter the testing arena voluntarily or not, that change which behaviour is observed (for more see e.g., 'one test for many traits' in Carter et al. (2013); Perals et al. (2017)). Convention and convenience play a too important role in behavioural testing, resulting in researchers rarely validating established methods for their appropriateness in given study organisms or research questions. Using non-standard behavioural testing paradigms, such as mesocosms, demands a critical examination of a chosen experimental approach. Although some view potential ambiguities in non-standard approaches as weaknesses, I see them as valuable reminders to think critically and to remain humble.

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I now illustrate in more detail, with examples from my work, how exactly testing environments can matter. Firstly, and most obviously, the **ecological context matters for behavioural testing**. Heterogeneity and variation in the environment –typically reduced as much as possible in the lab– mediate behaviour. As an example, the water in the mesocosm can be turbid (depending on the season and weather) and light conditions vary naturally. In several species of fish, increased turbidity has for example been shown to result in increased foraging activity, reduced shoaling behaviour, and reduced collective behaviour (Michael et al., 2021; Wishingrad et al., 2015; Zanghi et al., 2023). Such environmental variation often further limits the extend to which behavioural observations in fish can be carried out in the wild, such that experimental mesocosms, as used in this thesis, can be valuable for collecting data not otherwise obtainable in laboratory or field settings.

More importantly than changing the expression of behaviours, **heterogeneous environments allow for the expression of a wider range of behaviours**. By reducing the visibility to predators, more turbid, or darker environments may allow for the expression of anti-predator behaviours other than shoaling. Similarly, in most of our mesocosm experiments, we provided shelters, such that hiding presented an alternative anti-predator strategy. The existence of such alternatives, resulting from environmental heterogeneity, reduces the dependency on certain behaviours (here: shoaling for protection), and thus allows alternative behaviours to be expressed.

In light of these points, the actual lesson is that **the existence of alternative options matters** when assessing behaviour. In our experiment presented in Chapter 3, we surprisingly found that stickleback rarely moved in groups when crossing between ponds of the mesocosm (Gismann et al., 2024) which contrasts with the vast majority of the literature on stickleback shoaling behaviour. Indeed, in the mesocosm, groups typically split such that fish moved alone most of the time. Furthermore, in (semi-) natural environments, fish can actively select their social partners ('(social) niche choice'; Stamps and Groothuis (2010)) which provides them with control over their environments, rather than being forced to adopt the behaviour of others due a lack of alternatives. This indicates that **alternative social options matter** and hence, future behavioural studies should be designed to provide alternative options and to allow for freedom in individuals' choices.

In fish, individual propensity to shoal or social preferences have largely been studied in the lab using binary choice tests (but see Krause et al., 2000; Ward et al., 2017). In choice tests, individuals are placed in an empty test tank and then presented with a binary choice (e.g., two individuals behind a transparent partition on opposite sides of the tank or a group of fish on one side and an individual (or smaller group) on the other side). The time spent on one side over the other then serves as the outcome parameter. Similarly, in studies on collective behaviour, groups of fish are often placed in small and often empty testing arenas. While laboratory tests of that nature have proven to be useful tools (Herbert-Read et al., 2011; Katz et al., 2011), their validity outside the specific testing paradigms is only rarely tested. Therefore, caution is warranted when extrapolating from observations in laboratory setups to behaviour in the wild (Krause et al. (2000)). To accommodate alternative social options, in Chapter 5, we studied stickleback social behaviour, using an experimental setup designed to allow individuals to freely express their association preferences. The setup was larger in spatial scale than any of our previous experiments, and contained large numbers of fish, to allow for spatial structuring of individuals and social groups.

I believe, that, owing to the lack of alternative (social) options and limited environmental variation, one can draw similarities between laboratory tests in animal behaviour and e.g., high-dose or 'supraphysiological' medical studies, where doses of hormones or toxins are administered that are vastly higher than typically experienced by the organism. Such studies are useful in eliciting the general breath of effects and underlying mechanisms, yet often fall short in describing real-world scenarios.

Beyond the question of whether laboratory observations reflect behaviour in ecologically relevant conditions, there is a risk of overestimating the strength of results from lab tests when subjects lack alternative behavioural options. In Chapter 3, for example, we found that social conformity influenced the behaviour of individuals less than expected and that individuals largely expressed their intrinsic movement tendencies. Contrary to our expectations, we did not find that fish responded to the behaviour of the majority of their social group. Social effects, such as social conformity, are shaped by the ecological context and individuals often respond to their group mates stronger in risky environments (Ward and Webster, 2016). It is plausible, that environments which more closely resemble natural environments (e.g. regarding environmental structure and variation) are perceived as less dangerous than many laboratory setups. In setups perceived as safer, the balance between the costs (e.g., increased risk for pathogen transmission Krause et al., 2002; Albery et al., 2021) and benefits of social associations may shift, such that individuals become more solitary. In the mesocosm system, individuals may more often chose to move and explore alone –which may be less efficient than in a group (Dall et al., 2005)–, to reduce the amount of conspecific competition during foraging (see Intermezzo 1 for another example of how environmental conditions mediate the costs and benefits of social associations).

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The experiments conducted in the mesocosm system were much larger in spatial scales than classical (and my own) laboratory experiments. My next learned lesson is thus that **spatial scales matter**. In our first mesocosm experiment, presented in Chapter 2, we discovered differences in movement behaviours between resident and migrant sticklebacks only when testing fish on large spatial scales (Ramesh et al., 2023). Most classical behavioural studies would not have allowed testing on such spatial scales. Without the larger-scale test in the mesocosm, we may have erroneously concluded that, despite marked differences in life history, the two populations did not differ in their movement behaviours. Even more so, when tested for activity in the lab, it was residents that moved more than migrants (Ramesh et al., 2021). Although movement in a small laboratory tank clearly differs from movement in a large mesocosm, distinguishing between seemingly similar behaviours is not straightforward. Behaviours that may seem similar, can be functionally distinct depending on the spatial scale of testing. For example: Movement in an empty lab tank is typically described as 'activity' (I will discuss the interpretation of this behaviour later), whereas movement between ponds of the mesocosm in Chapter 2 and Chapter 3 may best be described as 'migration-like'. While these movement behaviours are clearly functionally

distinct, it is difficult to categorize intermediate behaviour such as movement within ponds (measured in Chapter 2).

The next lesson is that **temporal scales and the timing of testing matter**. During our mesocosm experiments, we tracked the movement of individuals for a minimum of several hours (16 hours in case of Chapter 2 and Chapter 3) and up to several weeks (Chapters 4 and 5). For example, if strong shoaling behaviour in the lab represents a temporary stress response to a novel environment or handling, behavioural tests over substantially longer time scales could alleviate initial stress and further reveal otherwise hidden temporal changes in behaviour.

In Chapter 2, we were specifically interested in migration-like movement, such that we tested the fish during the stickleback migratory season in spring. Whether observations of the same movement behaviour outside of the migratory period still represent migration-like behaviour is unclear.

All of these lessons for behavioural testing can maybe best be summarized by the fact that **it is crucial to consider the ecology and life-history of ones study organisms**. Laboratory setups by definition remove an organism from its natural environment. This means that one needs to be careful in determining whether animals can adequately express the behaviour that one aims to measure and one needs to be aware that in real-world scenarios individuals might display behaviour markedly different from the one observed. Broadly speaking, organisms dramatically differ in ecology and life-history. This applies across all levels of organization, from species, to populations, to individuals within populations. Because standardized laboratory tests are designed from a researchers perspective rather than from the organisms perspective, one risks measuring behaviour that lies outside the behavioural repertoire of the study subjects (Berman, 2018). Ramesh et al. (2022), for example, followed standard laboratory methodology to assess *activity* in fish (measured as distance moved in an open-field trial in a specific time interval). and, as previously mentioned, found that resident sticklebacks moved much more than sticklebacks from a migratory population. These results were unexpected and because migrants barely moved at all, Ramesh et al. (2022) suggested that migrants may have displayed freezing behaviour. Freezing behaviour is an alternative anti-predator strategy in fish in the absence of a social group (Huntingford and Wright, 1993). By testing individuals isolated from their social group, rather than reflecting activity, the behavioural tests might thus have elicited anti-predator behaviour in migrants. Due to differences in social system and/or anti-predator strategies, individuals from

resident and migrant populations may have perceived the same behavioural test differently, highlighting the importance of considering the ecology of ones study organism.

By using behavioural testing paradigms that more closely resemble the natural environments of study organisms, researchers can avoid some of these issues and reduce reliance on often unclear assumptions about the suitability of their tests.

These lessons are not meant to invalidate or question classical laboratory studies in general. Instead, I aim to show how mesocosms and similar alternative experimental paradigms can complement, validate and expand findings from traditional study approaches in behavioural biology. Behavioural tests in the lab can very well correlate to or predict outcomes under (semi-) natural conditions (Klaminder et al., 2016; Krause et al., 2000). For example, I have shown in Chapter 4 the existence of a positive relationship between activity and aggression tested in the laboratory, and dispersal and mating success measures in semi-natural conditions. My points are thus, that we should be cautious in assuming laboratory findings translate to the wild, that the strength of effects observed in the lab may be diminished in ecologically relevant environments, that absolute differences between individuals or groups might differ in the wild or even be reversed, and that given the vast diversity in organisms' ecology, efforts to generalize laboratory findings must be undertaken carefully. Fueled by similar considerations as well as advancements in tracking technologies, scientists in many fields are again moving towards studies in the wild or semi-natural settings (King et al., 2018; Spiegel et al., 2017; Hertel et al., 2019, 2020).

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BEYOND METHODOLOGY- CONCEPTUAL DIFFERENCES

Studying behaviour in freely moving and interacting individuals in (semi-)natural environments, differs significantly from traditional methods, both methodologically and conceptually. This approach recognizes individuals' agency and embraces ecological complexity—including both physical and social environments—as crucial components of the organism. This shifts perspective from the researchers to the organism, recognizing the importance of observing individuals' behaviours in the context in which and for which they have evolved. Furthermore, by recognizing that individuals do not merely differ in behaviour, but that the reasons for such differences often lie in how individuals perceive and interact with their environment, one explicitly tries to put the individual first.

The data collected in experiments set up according to these principles are typically complex. In semi-natural conditions, the wide range of potential factors influencing measured outcomes often creates ambiguity about the underlying mechanisms. For example, in Chapter 3, we cannot conclusively answer which factors best explain the weak social effects observed. Yet, this complexity created opportunities to explore the data more widely, potentially uncovering unexpected observations. Such complex data thus encouraged us to go beyond simple summary statistics. In Chapter 4, for example, we were not only able to show how personality variation can relate to fitness proxies, but also obtained highly detailed observations on the dynamics of male-male competition over breeding territories (e.g., how fast and for how long males establish territories, territory conflicts, territory take-overs), something we originally did not plan to investigate. Many of these observations were obtained after extensive data exploration and visual inspection. This was possible, because our experiment was designed for open-ended data collection, extending beyond the main outcome parameters. As a result, most of the data generated over the different experiments during my PhD could be re-analyzed for a wide variety of fascinating research questions, such that our studies are more exploratory than they may originally seem. Overall, the experiments contained in this thesis provide highly detailed insights into stickleback behaviour in a system where laboratory observations have limited ecological validity, and field observations typically do not provide data of the same level of detail. In Chapter 5, for example, we were able to continuously track the behaviour and social associations of all individuals in the experimental population over several weeks and independently of the time of day, or visibility in the water. Comparable data are extremely rare in fish behavioural studies, to the exception of tracking studies using high-resolution acoustic telemetry systems Aspillaga et al. (2021), Nakayama et al. (2016), or Villegas-Ríos et al. (2017).

Currently, mesocosms allow the collection of data otherwise impossible in fish. Yet, as tracking technologies advance, we will be able to address increasingly more questions directly in the wild, such that I expect a 're-wilding' of behavioural studies in the future. Owing to the nature of the underwater environment, and its unique challenges, these technical advancements seem to be progressing slowly, such that mesocosms should be embraced as valuable tools in expanding the methodological arsenal for behavioural research in fish. Furthermore, for some experimental approaches, mesocosms may remain invaluable, such as for example when aiming to perform controlled environmental manipulations under ecologically relevant conditions (similar

to Chapter 5).

SOME PROBLEMS WITH THEORY IN BEHAVIOURAL ECOLOGY

6 While a strong theoretical foundation is crucial for explaining the natural world, I find the current application of theory in hypothesis-driven research problematic. Scientists are taught to design experiments to test specific hypotheses. These hypotheses derive from theory. Yet, from my own experience, I think too many empiricists are predominantly exposed to theory through other empirical work. These works typically mention theory only briefly before focusing on hypotheses to be corroborated (something along the lines of e.g., "life-history theory predicts that high mortality should lead to the evolution of shorter lifespans and more risk-prone individuals"). In practice, theory is thus often reduced to simplistic verbal arguments, which become empty shells. When theories erode this way (not necessarily the theory itself, but the way it is understood in practice), they might eventually substantially differ from their original. Scientists furthermore run the risk of inadvertently ignoring a theory's assumptions and intended scope ('boundary conditions'). This risks formulating incorrect hypotheses or testing on systems not suited for the questions at hand ('conceptual stretching' Grainger et al. (2022)). If hypotheses are then for example not corroborated, scientists may erroneously question the theory, or reframe their results to support the theory, even when the theory should never have been applied to the given study system. These remarks are meant to call for a stronger emphasis on theory and the science of philosophy in teaching curricula in (behavioural) biology and for closer collaboration between theoreticians and empiricists. In a recent preprint Nakagawa and Lagisz (2024) describe related issues of communication failures between empiricists and theoreticians, and invoke the term of a 'theory crisis' in biology. They argue that a lack of theoretical understanding, weakly described or vague theories, as well as a general shortage of theoreticians, can be a major contributor to research waste in the biological sciences. In the field of ecology, research waste already today presents a major challenge (Purgar et al., 2022).

FUTURE DIRECTIONS IN BEHAVIOURAL ECOLOGY

In my view, the most crucial aspect for future studies in behavioural biology is considering individuals' ecology during behavioural testing. As explained in my 'lessons learned', I refer to ecology in a broad sense, covering an animal's past and current environments. My learned lessons largely parallel the Eco-Evo-Devo approach described in the introduction of this thesis (and in

the grant proposal on which my PhD was based), which can be summarized as follows: Understanding in behavioral biology requires considerations of the environments in which animals' behaviours arose ('Evo'), are shaped by ('Devo') and are expressed in ('Eco'). Such an approach can take several different forms. Whenever possible, behavioural studies should be performed in the wild. While currently many questions can not yet be answered in the wild, innovations in tracking technology will expand the scope of possibilities. Alternatively, studies could be set up, such that field and laboratory approaches are combined. When performed in the laboratory, studies should be tailored to the study organism to a larger extent than currently the . Lastly, mesocosms can be valuable tools, by balancing many of the benefits and drawbacks of laboratory studies and studies in the wild. The variety of mesocosm setups used in this thesis and the types of questions we were able to address, highlight how useful comparable semi-natural systems can be for behavioural studies. I thus believe that to date, these are underutilized in behavioural ecology.

Furthermore, I believe future studies will become more open-ended in data collection, due to advances in, for example, tracking technology. By going beyond single outcome parameters, (future) 'big-data' behavioural studies allow and should focus more on the wide exploration of the collected data. Scientific understanding commonly arises when natural observations are formalized into theories, from which testable hypotheses can be deduced, which are subsequently tested in hypothesis-driven research. Today, the balance between these necessary steps has very much shifted toward the latter, with hypothesis testing, or 'confirmatory' studies, largely dominating the field of ecology. In turn, descriptive and exploratory (non-confirmatory) approaches have come out of fashion. I believe that descriptive work through open-ended behavioural observations still offers numerous opportunities for discovery, and that an excessive focus on hypothesis-driven research, especially in a publish-or-perish culture, fosters questionable practices like cherry-picking of statistically significant results, hypothesizing after results are known (HARKing), and p-hacking (Fraser et al., 2018). Descriptive or exploratory studies, by nature, do not rely on the confirmation of pre-formulated hypothesis and should therefore be less prone to questionable research practices, potentially resulting in lower publication bias. Such studies furthermore actively encourage to take a variety of factors into account, or ideally, are performed in the animals natural environment. I thus believe that funding agencies and scientific publishers should allow more room for descriptive and exploratory studies, especially in the wild. Incentivising this type of work is important

for researchers to re-engage in the necessary first step of scientific discovery.

Besides methodological and conceptual differences, one scientific area that seems under-explored in behavioural biology, especially in fish, is animal behaviour in a multi-species context. Beyond the predator-prey context, behavioural interactions between different species are rarely studied. Fish, for example, seem to have a remarkable ability to form (social) groups that consist of several species. This becomes apparent to everyone who observes fishes in their natural habitat. Not only does this apply to species-rich tropical reefs, where such a phenomenon might be expected, but many other aquatic environments too. Three-spined stickleback in our system, for example regularly associate with nine-spine sticklebacks (*Pungitius pungitius*) (pers. observation). Multi-species shoals often occur just as regularly, or even more commonly than single-species shoals (Krause et al., 2000; Hoare et al., 2000), prompting interesting questions about their function and consequences for ecology. While for strongly shoaling species, these interactions may predominantly serve anti-predator functions ('safety in numbers'), interactions with heterospecifics are instrumental in the context of resource competition even for solitary species.

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Especially from an animal personality perspective, many fascinating questions arise. Given the breath of ecological and evolutionary consequences of individual behavioural variation within populations, it is reasonable to assume that individual variation in behaviour between several closely interacting species should similarly matter. How, for example, does multi-species individual variation in behaviour play into the detection of predators or resources in the environment? How does it affect dispersal when more than one species disperse? How does it affect survival in a drying intermittent river where fish have to find refuge pools? How, in a social context, do multi-species interactions change our view of animal cognition, when individuals need to assess and appropriately react to behaviours of conspecifics and heterospecifics?

In 1963, Tinbergen formulated the Ethologists' desire to '*return to nature*' –similar to the one I feel today– as follows: "*return to nature was a reaction against a tendency prevalent at that time in Psychology to concentrate on a few phenomena observed in a handful of species which were kept in impoverished environments, to formulate theories claimed to be general, and to proceed deductively by testing these theories experimentally [...] and was soon losing touch with the natural phenomena*". My call for more exploratory work in animals' natural environments is thus not novel, and probably neither contended among ethologists, yet many of the most recognized and celebrated

advances in behavioural studies seem to move in the opposite direction: rather than trying to explicitly incorporate an individual's environment with all its intricacies and dynamic interactions, we increasingly employ complicated statistical methods to derive minute differences, too often without considering how these might translate to behaviour in the wild.

So, let us try to return to nature once again.

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