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Adaptation and Learning in Fish: Effect of individual behavioral and informational variation on collective outcomes

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Anpassung und Lernen bei Fischen: Auswirkung von individuellen Verhaltens- und Informationsunterschiede auf das Kollektiv

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Summary

The work presented in this thesis set out to test various forms of learning and behavior adaptation. The bulk of this work was done using a naturally occurring clonal fish species, the Amazon molly *Poecilia formosa*. This sociable, all female species produces genetically identical offspring through asexual reproduction. With the advent of increasingly detailed approaches to discriminate behavioral differences, such clonal species are vital in ethology as they serve as a perfect natural model to test for individual behavioral differences and the development of such. Since genetical variation can largely be excluded as a confounding factor, attention can be drawn towards the differences among individuals due to their prior experience. In the first three chapters of the work presented here, the individual information and experience was altered by applying operant conditioning or by exposing the animals to novel or well-known situations. This was done both individually and in a group setting. By doing so, the effect of the social context, as well as the physical surroundings on behavioral aspects such as swimming speed and jumping probability was determined. Minute behavioral differences were then evaluated in the following chapter by comparing manual approaches and automated quantification tools. Lastly, a methodological approach was taken in which the power of artifical neural networks was harnessed to track individuals in convoluted natural scenes during predator-prey interactions.

Zusammenfassung

Die in dieser Arbeit vorgestellten Arbeiten zielten darauf ab, verschiedene Formen des Lernens und der Verhaltensanpassung in Tieren zu testen. Hierbei wurder der Großteil dieser Arbeit an einer natürlich vorkommenden klonalen Fischart, der Amazonas-Molly Poecilia formosa, durchgeführt. Diese gesellige, ausschließlich weibliche Art erzeugt durch ungeschlechtliche Fortpflanzung genetisch identische Nachkommen. Mit dem Aufkommen von immer detaillierteren Ansätzen zur Unterscheidung von Verhaltensunterschieden sind solche klonalen Arten in der Ethologie von entscheidender Bedeutung, da sie als perfektes natürliches Modell dienen, um individuelle Verhaltensunterschiede und deren Entwicklung zu testen. Da genetische Variationen als Störfaktor weitgehend ausgeschlossen werden können, kann die Aufmerksamkeit auf die Unterschiede zwischen Individuen aufgrund ihrer Vorerfahrungen gelenkt werden. In den ersten drei Kapiteln der hier vorgestellten Arbeit wurden die individuellen Erfahrungen durch operante Konditionierung oder durch das Aussetzen der Tiere gegenüber neuen oder bekannten Situationen verändert. Das jeweilige Verhalten wurde sowohl alleine, als auch im sozialen Kontext untersucht. Auf diese Weise wurde die Auswirkung des sozialen Kontexts sowie der physischen Umgebung auf Verhaltensaspekte wie Schwimmgeschwindigkeit und Sprungwahrscheinlichkeit ermittelt. Kleinere Verhaltensunterschiede wurden dann im folgenden Kapitel durch den Vergleich von manuellen Ansätzen und automatischen Quantifizierungsinstrumenten bewertet und evaluiert. Schließlich wurde ein methodischer Ansatz augearbeitet, bei dem die Leistungsfähigkeit künstlicher intelligenz in Form von neuronalen Netze genutzt wurde, um Individuen in komplizierten, natürlichen Szenen während Räuber-Beute-Interaktionen zu verfolgen.

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"Throughout our daily lives we are confronted with known and unknown, as well as pleasant and un-pleasant situations. We go about our routines and traditions, take both the past and the present for granted and may not even be aware of any changes taking place. Surely the seasons can be experienced and one can determine a scholar from a novice, but the exact point in time at which one is found and the other has left remains uncertain. Thus, we are reliant on external sources such as the position of the sun in the short winter days or the sound of a note played to perfection to gain more information about the state of our surroundings. We ourselves hold information as well. Experience, ingrained and stored among our cells over a lifetime allows us to compare - known against unknown, comprehensible against confused, predictable against uncertain. Alas, it is us who carry a piece of the world inside us. Like the vikings using their sunstone to find their path in unforseeable weather, we navigate our way from the naïve infantile darkness to enlightenment and death clutching our own internal and imperfect reference. Let this be a story of learning..."

- Myself, 2023

1. Introduction

As a highly social species ourselves, human curiosity has long been drawn to other aggregates of animals and the intricate forms these may take on. Observing the flight of a flock of starlings or the highly synchronized motion of a school of sardines has hypnotized humans for centuries. More recently the concepts regarding individual interaction rules and underlying processes governing the collective behavior of such groups have been studied in much more detail [127, 53, 226, 104]. This has lead to the emergence of the interdisciplinary research field of collective behavior which bridges many scientific domains such as biology, psychology, computer science, robotics and engineering. The interdisciplinary nature of the research area is given by the fact that any system comprised of interacting but individualistic units can be seen as a collective. Understanding the evolutionary history of such systems in nature can therefore give insights into the optimal information sharing strategies [111], space use approaches [133] or decision making processes [145]. These insights can then be applied in designed systems of our own, such as networks of independent servers or self-driving vehicles [182]. Not only is this field of research important for engineered aspects of our daily life, but also has shown to be applicable to other decision-making and consensus processes in human societies [89]. In this thesis the biological aspect of learning and adaptation was evaluated in more detail, spanning from individual to group level behavior. This was done by using social fish species, which represent a biological form of multi-agent system with individuals interacting on a collective level to acquire information, find a food source or seek shelter. To date, both the proximate, as well as the ultimate aspects of behavior have been studied at the individual level [92, 138] and at the collective level [127, 90, 212]. Yet, an unified understanding of benefits and costs of group heterogeneity and individual variation across various contexts is still missing [104].

The overall goal of this work therefore was to extend the research combining both individual aspects and group aspects at the same time. Work such as that by Herbert-Read et al. [90], MacGregor and Ioannou [147] and Jolles et al. [104] has achieved some remarkable insights in this direction, on which the work presented here heavily built upon. In order to achieve both individual and group level insights at the same time some novel methodological approaches are necessary. As part of this work, state-of-the-art techniques to record animal movement and behavior were incorporated and evaluated. Technological innovations as such can be used to bridge certain aspects of individual and group level quantification in both the lab environment and natural surroundings of animals.

In more detail, the questions of interest in this piece of work focus mainly on the ability of individuals to learn and adapt to novel situations and conspecifics, and how

to quantify such behavioral changes - How do individuals address the trade-off between acquiring information alone and spending time with others? Which behavior is socially mediated and why? How can minute behavioral changes be determined by an observer? How can we bridge the gap between controlled, lab based experiments and natural behavior in the wild? These questions were addressed by designing experimental paradigms in a laboratory setting and developing novel methods of behavioral quantification. Such methods allow for standardization of scientific procedures and ensure reproducability across observers, experiments and model species [33]. Given that individual and group level aspects were of interest, many of the experiments presented here were done using the naturally occurring, clonal, live-bearing fish species the Amazon molly *Poecilia formosa* (Girard, 1859). Using such animals as model organism further reduces confounding effects which would otherwise arise due to genetic differences among individuals [140]. Behavioral differences were quantified using manual observations, as well as computer assisted techniques to track the individual's position and body posture over time. These behavioral descriptors in form of coordinates were then analyzed as time series from which behavioral traits such as swimming speed or learning efficiency were derived. This allows for behaviors to be resolved on a high spatio-temporal scale, by which timing of events and their consequences can be distinguished and analyzed in the given context.

The structure of this thesis is the following. First, a historical background is given, covering some of the most important concepts of animal learning and adaptation. In the first empirical work shown in chapter 2, aspects of individual and social learning are tested, such as the cost of varying information among social partners. Following such learning paradigms at the individual level, aspects of social contagion of behavior over time are highlighted (Chapter 3). Given that individual behavior is shown to be effected by the social context, the effect of social and physical environment on the behavioral adaptation at the individual and group level were tested over a longer time scale (Chapter 4). Effects of temporal changes in environmental variation were then further tested by exposing individuals to differing feeding regimes and food availability and repeatedly measuring certain behavioral traits, such as motility (Chapter 5). Lastly, in chapter 6, methodological tools which were developed to determine minute behavioral differences using algorithmic approaches (Section 6.1) and detect and track multiple individuals in complex natural scenes in the wild (Section 6.2) are introduced and evaluated.
Overall, the results of this work support the findings of previous work on consistent behavioral differences in animal behavior, showing that it is present in various situations and traits [67, 90, 138]. In the here presented work, an aspect found to greatly effect these differences is time. Over time habituation, adaptation and learning can take place, by which information is acquired which in turn alters the behavior of an individual. Measuring and evaluating these behavioral changes

over time can be difficult, due to the gradual transition and unknown onset. With computational power readily available, behavior can now be quantified continuously and over various time scales, using highly specialized techniques [33, 230]. These include tracking an animals behavior as body position and posture[1] over time and allow for changes in behavior to be detected and analyzed. As part of this body of work, methodological advances were implemented and tested which allow the classification and quantification of behavior on a sub-second level. Although not unique to this work (see Berman et al. [22], Brown and de Bivort [33]), it is a highly valuable tool in order to analyze and predict behavioral phenotypes and changes in such [168]. This in combination with the established work on collective behavior [127] gives rise to a plethora of questions on how individuals aggregate, and what choices are made when doing so, while being behaviorally heterogeneous. Many of such questions can likely be addressed in real-time and pave the way for an exciting future of ethology [109].
To give an introduction into the bulk of the field of animal learning, main concepts and key ideas which are fundamental to the here presented work are highlighted in the following section.

1.1. Background

Learning, adaptation and habituation can be difficult concepts to disentangle, where each has been studied to great extent [143, 32]. All aspects have however one key criterium in common, as they are all time dependent processes, making them challenging, yet fascinating to study. In the following, emphasis is placed on animal learning and adaptation, as these are two means by which an animal can react to changes within the proximate environment, alter the information it acquires and change its behavior over time [143, 32].

As Miller and Dollard [158] concluded in 1941, the concept of learning can be described as follows: "[...] in order to learn one must want something, notice something, do something and get something." This simplistic, yet sufficient statement is a good starting point for understanding various forms of learning, which exist across the various fields of research, such as biology, psychology, informatics and engineering. This concept further gives a distinct approach to the understanding of behavior and, more generally, to the processes that may drive its evolution.
Defined in more clear terms, the *Four Fundamentals of Learning* have been described by Miller and Dollard [158] as drive, response, cue and reward. A certain behavior can be defined as a goal directed action, based on intrinsic motivation with some

[1] Specific terms and key concepts are highlighted and further explained in the separate glossary section A.1

mismatch between realized goal and anticipated goal [87]. Series of such behaviors have been suggested to follow a hierarchical structure, allowing for continuous adaptation and dynamic response to changing circumstances [137, 57]. Together, this can be formulated as a working definition of learning as "An incremental, goal oriented behavior, intrinsically motivated by a given state (drive), by which the environment is sensed (cue) and acted upon (response) resulting in a new intrinsic state (reward)". However, learning only applies if the initial state ("want" or drive) and the new intrinsic state ("get" or reward) are not identical. Only then can an informational gradient be detected and acted upon (learnt). The opposing case of no gradient being present does not allow for any difference to be noticed or acted upon, and therefore merely facilitates identical behavior or continuation, and does not require the behavior to be updated or changed. The process of learning therefore describes the minimization of error between a predicted and an actually realized outcome.

In a more biological sense, the ability to learn has been recognized to depend heavily on the species, its ecological context and an individual's internal state, as well as the utility of the resulting behavior [180]. Given these constraints, the learning abilities are not easily generalized across taxa, let alone tested on a common scale [217, 29, 30, 180, 61].

The ability to learn likely shares the same fate of being under constant selective pressure, as any other individual trait on which evolution can act upon [30, 47, 177]. Conceptually, individuals can acquire information directly by interacting with their environment [54] (i.e. individual learning see Glossary) or by observing others in a social context (i.e. social learning) [12]. The concept of a theory of mind and other forms of mental representations allow for the internalization of possible realities and their outcomes, and for conceptualizing reactions [69, 128]. The information gained through individual experience is commonly referred to as private information, if acquired alone, and public information, if accessible to, and acquired by many [158, 54]. Further, a distinction between the sources of information can be made, separating low correlation cues (e.g. a small, barely visible light source) providing private information from high correlation cues (e.g. a loud sound) which provide public information [111]. In accordance with B. F. Skinner, cues can further be categorized into positively and negatively reinforcing, depending on whether they lead to aversive or pleasurable consequences [203, 74].

For centuries, the concept of intelligence has been of interest to psychologist and biologists alike. The great philosopher Aristotle took interest in animals and their intricate behaviors and Darwin himself systematically observed and documented animal behaviour and contributed intelligence, which he published in his book titled *The Descent of Man* [55]. After Darwin's death, much of his work on this topic was revised, extended and published later by George Romanes [188, 189]. In response, Romanes received harsh criticism by Conway Lloyd Morgan, who rigorously revised

and tested many of the statements and assumptions proposed by Romanes [160]. Sparked by these insights at the time, Thorndike most famously proposed a series of experiments to understand the mechanisms behind "animal intelligence" and, more accurately "learning" [217, 218]. He tried to systematically compare animals based on their learning abilities by having them perform analogous tasks. These experiments aimed at testing the prevailing opinion that there must be a common process defining learning in all organisms. His insights led him to conclude that learning took place in a gradual manner, could not be facilitated by imitation and that no complex cognitive abilities were at play. Although the comparison across taxa could not easily be done, he further suggested that some properties at play during learning may be the same across species [217, 218].

Today we know that learning can in fact be facilitated by imitation [43] and that the degree of cognitive abilities may scale with the complexity of the corresponding actions to be learned [180, 42, 14]. Thorndike went on to formulate his law of effect, according to which behaviors followed by positive reinforcement are strengthened and those followed by negative consequence weakened [217]. Simultaneously, physiologist Ivan Pavlov laid out the fundamentals of classical conditioning in 1897, by initiating salivation in dogs in response to a bell [170]. These experimental findings were further refined and published in 1913, marking the advent of modern Behaviouralism with Watson [232] and later Hull [95, 96, 98], who famously coined the systematic behavior or drive theory in 1943 [97]. B. F. Skinner built upon these insights and later defined operant conditioning, also known as instrumental conditioning, as extended form of learning, where positively reinforced behavior is more likely to be repeated and negatively punished behaviour is less likely to be expressed [203]. In other words, an animal learns to associate a specific behavior (such as pressing a lever) with a consequence (such as receiving a food reward), resulting in a subsequent increase or decrease in the frequency of that behavior[2].

Learning has historically been the tackled by the fields of biology [217, 221, 144], comparative psychology [98, 200] and anthropology alike [222], which have concluded that learning enables individuals to adapt to their environment within their lifetime or shorter, and solve problems which they encounter repeatedly. Thus, learning is the fastest way an individual can cope with repeatedly occurring environmental changes. Hence, the ability to learn should be under strong selection pressure as individuals that can learn are predicted to outcompete those that cannot. Ultimately, the ability to learn then increases an individual's Darwinian fitness and proximate adaptability. This process has been nicely conceptualized by Plotkin [177], where the hierarchical levels of information acquisition and storage across various spatio-temporal scales is demonstrated. In biology learning situations can generally be seen as all "problems that animals encounter repeatedly and that can be solved by learning", which was

[2]For further information on the topic of learning theory see Hull [98] and Byrne et al. [43]

adapted from Bitterman [29] and of which some of the general categorizations are described as follows.

1.1.1. Individual Learning

Various forms of learning exist which have historically been discussed and categorized, where the learning mechanism may be the main mean of differentiation [192, 185]. Further, internal as well as external constraints influence the form of learning which is most effective under any given circumstances [199]. In simple cases, such as those eluded to by the work of Pavlov [170], Thorndike [218] and Skinner [203], individual learning takes place by sequential trial-and-error. Individuals acquire information alone, in absence of social cues and without any influence from others. An individual attempts an action and by doing so receives positive or negative reinforcement. A second form of individual learning is termed discrimination learning, where a distinction between varying stimuli needs to be made [98]. Both forms of information uptake lead to associations (good or bad) that further reinforce and condition the learning process towards a specific outcome [96]. Here, independent stimuli have independent reactions. The training is often achieved in a massed or spaced manner, in which training instances leading to reinforcement are either continuous (massed), or spaced randomly or intermediately with periods of no training taking place (spaced) [98]. The reinforcement does not necessarily lead to a single, task specific outcome (auto-shaping), but is highly dependent on the circumstances, the individual and the species in which conditioning takes place [37].

1.1.2. Social Learning

Social learning, or observational learning refers to the process by which an animal learns from the observations or experiences of others. The transfer of information in these situations is often affected by social facilitation, local enhancement and imitation [158, 93, 227, 143]. As the term suggest, social facilitation describes the process by which the presence of social partners enables an individual to perform better than when alone [244]. Local enhancement refers to added emphasis given to certain stimuli or informational cues in proximity to other individuals [220]. Individuals within a social group continuously face the choice of acquiring information directly or gaining it through others, via social learning. This conundrum, at the individual level between exploring in order to gain better information and exploiting the already known sources, leads to the public goods problem known as the exploration-exploitation dilemma at the level of information [150, 223]. Exploitation, in this case refers to the processes of social learning, which has been observed in various non-human animal societies [73], and human social systems [12, 13]. Exploration

refers to the process of acquiring information alone [170, 218, 203]. Once skills or other manifestations of information can be socially acquired, they can be passed on over generations leading to the cultural transmission of information. The information being transmitted by means of social learning is diverse, including song types [75, 76], foraging techniques [115, 6, 9] and food preferences [131]. Commonly it is beneficial to the individual to acquire knowledge through social learning, as it removes the need to test all possibilities alone. However, this form of learning need not only be positive, but can also lead to maladaptive behaviour [134] or be associated with certain costs, such as increased energetic effort [133], misinformation [80] or decrease of biological fitness [176, 201]. Nonetheless, the mean of informational exchange through social transmission and across generations (aka. culture) is of such importance to gregarious animals, that it has been suggested to act as a 'second inheritance system' in parallel to genetic evolution [47].

1.1.3. Collective Learning

Individual learning theories are limited when it comes to assessing a multi-agent system, or group of animals, as a learning system itself [113, 120]. Yet, evidence exists that group dynamics do not merely reflect a summary of all its individuals characteristics, but that each group has entirely new, yet consistent traits. This congruent evidence comes from work on fish schools [146, 105] as well as human groups [241] and leads to the assumption that a further form of learning may also be at play, namely that at the system level [120].
The formulation by Kilgore [120], coming from a sociological perspective, describes a process by which a collective, defined by its collective identity and consisting of unique individuals, is acting towards a common goal. Information can be seen as a resource which is spatio-temporally distributed [167], and ambiguously (public) or locally (private) preserved [111]. On a higher level interpretation, the information is stored within a system with memory capacity (i.e. single agent, multi-agent collective or group) [179] and transported through time and space. As information is encapsulated within these systems, they can be seen as information vectors [81]. Within the collective, both the common goal and the information available to each member is subject to individual interpretation and experience, which leads to variation and group heterogeneity under the unifying umbrella of the collective identity [120]. Recent research has further elicited that collective learning may be induced by social learning [126], alluding towards a more continuous and less categorical difference between social and collective learning.

1.1.4. Learning Processes

A learning process can be seen to be comprised of a learning situation (i.e. the situation that requires learning) and the learning phenomenon (i.e. the means by which learning takes place). Let us consider a simple learning process as example, which is given by classical conditioning in accordance to Pavlov [170]. An individual is conditioned on an association between a neutral stimulus (e.g. light, sound) and an unconditioned response (e.g. salivation, flight). In this case the learning situation is given by the fact that a connection between both stimuli and response needs to be made. The learning phenomenon is an individual discrimination learning approach, given that the correct stimulus needs to be discriminated and learning takes place in absence of any social partners. In a second case of learning process based on the work by Laland and Williams [133], individuals acquire information about an optimal path to reach a foraging location. The learning situation is a spatial memory task, and learning takes place in a social context where the learning phenomenon is social learning via local enhancement.
In most learning experiments, the learning process that can be inferred from the learning performance or the data describing the performance is far removed from the actual learning mechanism [29]. A common process leading to such divergences is by one stimulus masking or overshadowing another [215]. Blocking takes place when the learning of component A of a compound task AB is reduced or compromised by the presence of B [215]. A further process effecting and often compromising learning data is habituation and adaptation, which can take place when the subject is repeatedly confronted with a situation or stimulus. Each confrontation with a stimulus leads to an altered reaction in any successive encounter where learning and habituation can be at play [216].

1.1.5. Adaptation

> *"The significance of an adaptation can only be understood in relation to the total biology of the species."* - Huxley et al. [99]

According to one of the most classical definitions in biology, adaptation is the fit between organism and their environment [56]. Interestingly enough the accounts of this predate Darwin and his book titled *On the Origin of Species* from 1859 [56]. Of such early accounts the most controversial view, otherwise strongly opposing those of Darwin, is the creationist philosophy. It suggests that organisms were designed by God to be best adapted to the environment they are placed in [202, 32]. While Darwin, partially opposed to such religious views, suggested an alternative mechanism of best fit via natural selection and evolution over generations. Others such as Jean-Baptiste Lamarck advocated for changes to take place on a much smaller time scale. According to Lamarck, individuals would adapt to their environment and the conditions they

face during their lifetime and pass these on via some mechanism. Today we know that this has been proven to some degree, when considering epigenetic alterations of the genome based on environmental effects which can be passed on to future generations. Darwinian fitness, or simply fitness refers to the reproductive success due to adaptedness of an organism to its surroundings. In the simplest form, a more adapt trait of an individual would lead to more offspring and higher fitness. In evolutionary terms such adaptive traits leading to differential reproductive success can evolve under natural selection and be subject to random drift before becoming fixed in the population. This is true for natural conditions under which populations sizes are finite. How strong the drift occurs highly depends on the population size and selection pressure acting upon the trait [32].

Much of the here presented work set out to highlight adaptedness in respect to behavior. The smallest unit that evolution can act upon is a population of interbreeding individuals. Such interacting individuals can gain adaptive superiority through fixed genetic pedigree or dynamic updating within their own lifetime through processes such as learning. This nicely closes the loop addressed in the here presented work, by which individuals have inherent differences (behavioral consistencies) which are affected by their experience and immediate Umwelt. The social and physical environment creates the link between individuals and allows for the exchange of information [240, 87, 111, 225]. Of course, the time scales taken into consideration in lab-based studies, as those presented in this thesis are arguably much shorter than those allowing for natural selection and fitness trade-offs to take place. However, incremental accumulation of experience and information can lead to sudden changes at a given point in time, or a single decision can have huge implications on future survival giving such smaller time scales great relevance as well [28, 225, 58].

2. Information Transfer and the Cost of Social Learning

2.1. Introduction

In 1514 Machiavelli already stated that "Men nearly always follow the tracks made by others and proceed in their affairs by imitation". This is not unique to humans alone, as many gregarious animal species often acquire information about their environment from their social partners [54, 79]. This process is commonly referred to as observational or social learning [28, 36, 233]. It contrasts private learning, where information is gained by exploring solutions alone and in absence of others [132, 111]. In general, social learning involves the observation of others and the copying of the their actions, where some produce information and others scrounge [73]. For example, task-naive Amazon Parrots (*Amazona amazonica*) have been shown to copy the behaviour of other, more experienced individuals in order to access an obstructed food source [172]. Reader et al. [183] demonstrated that wild guppies (*Poecilia reticulata*) could copy the food patch preference and predator avoidance behaviour from other conspecifics. However, how such social learning processes are affected by the initial skill levels of interacting individuals is only poorly understood. For one, social partners may differ in performance skills and thus in the quality of the information they can provide. Variation in information quality can in turn lead to error propagation and accumulation, giving rise to a potential trade-off between individual and social information use [80, 117]. Nevertheless, there is evidence that demonstrators' skill levels *per se* do not determine the extent to which they are copied by less experienced observers. For example, in the guppy, familiarity among individuals seems to be much more important than a demonstrator's skill when it comes to being copied [117]. Similarly, Roy and Bhat [191] found that utilizing social information led to food income equality in zebrafish (*Danio rerio*), where observers relied on visual behavioural cues of successful demonstrators to find food themselves. While these studies allowed for full contact among individuals and targeted leader-follower interactions, it still remains unclear how an individual's performance in learning a complex task by pure visual interaction with a partner is, in turn, affected by the partners performance skills. Nevertheless, some pioneering work has been done decades ago, on which the here presented work heavily builds on, investigating the relationships and potential costs and mismatches between observer and demonstrator [125, 23, 166].
Although numerous studies have highlighted the benefits of social learning to the observing or eavesdropping individuals as it allows an individual to circumvent

exploring all possible solutions on its own, and thus saves time and energy, e.g., opportunity costs are reduced [214, 234, 34, 36, 183, 117, 173, 85], these benefits might not be shared mutually with the observed and copied [224, 246]. While the mere presence of more individuals is beneficial during predator encounters [127], experienced demonstrators may lose task solving performance when interacting with inexperienced naive individuals, either due to distraction [191] or changed time budgets as more time is allocated to social interactions than to the task at hand [77]. But also direct negative effects of the copying behaviour are known. For example, in many fish species males copy the mate choice decisions of other males by observing these copulating with females which may help the observer determine high quality females. However, this behaviour will likely increase the risk for sperm competition and thus is costly for the copied male that initially mated with the female [174]. As a counter strategy, males may change their mate choices to mislead others and conceal their real preferences, which is referred to as audience effects [175, 247], a form of social deception [239]. In the context of learning a task by observation alone, the question remains of how the performance gradient among interacting individuals affects the outcome for all participants.

In addition to situations where there is an information discrepancy among individuals, social partners may also be faced with a counterpart with the same prior experience as themselves. Here, no additional task-specific, social information can be gained from observing such a partner, as the information would be highly correlated to the own experience and therefore deemed redundant [213, 111].

In the here presented study we aimed at testing how variation in skill levels between visibly interacting partners affected their learning performances (for those lacking prior information), as well as overall task performances (for those already experienced). We used the Amazon molly (*Poecilia formosa*), a naturally occurring clonal fish species that reproduces gynogenetically and gives birth to live offspring that are genetically identical to their sisters and mothers [194, 136, 209]. Through its clonal genetic background as well as its gregarious life-style, this species has been proposed to represent a useful model organism for the study of individual behavioural differences and the influence of behavioural traits on the social functioning of groups [59, 140, 141, 148]. However, to date no research has been conducted on the learning abilities of these fish. Due to this intricate natural history all individuals in this study were of same genetic composition and near identical rearing background. In a first step (private information acquisition), an operand conditioning procedure (5 days, 3 times training per day) was used to produce two differently experienced cohorts of otherwise genetically identical individuals: One cohort was trained to find food in a opaque cylinder (the task, see Figure 2) and therefore given the opportunity to learn to solve the task (task-experienced/trained individuals). The second cohort was trained to find food distributed randomly, with no ability to learn an association between food and cylinder location (task-inexperienced/naive individuals). In a

second step (social information acquisition), we paired two individuals to have visual access to each other, enabling them to observe each other while we continued (for trained individuals) or started (for those naive) the conditional training (5 days, 3 times training per day). Our full factorial design allowed us to create pairs of fish with all possible experience combinations: naive-naive, naive-trained and trained-trained. With this design, we tested first whether Amazon mollies are able to learn the task and whether there were consistent individual differences in both the learning rate and overall task performance at the end of the private information acquisition phase. We then explored how the skill level of the partner affected learning and overall performance when social information becomes available. The prediction was that naive fish paired with a trained partner will have a higher probability to reach a novel food source compared to individuals that were paired with another task-naive partner. For experienced Amazon mollies, the prediction was that the task performance would be worse when paired with naive individuals, compared to those interacting with a similarly proficient individual. The reasoning behind this assumption being, that individuals paired with a similarly skilled partner which provides redundant information may allocate more time and efforts towards acquiring private information - this can outweigh the potential opportunity costs that arise through the social interactions and which should be apparent when paired with both naive and experienced partners.

2.2. Methods

2.2.1. Study organism and maintenance

This study we used the Amazon molly (*P. formosa*), a naturally occurring clonal freshwater fish. This is an all-female species that originated from a rare hybridisation event between a male Sailfin molly (*P. latipinna*, ♂) and a female Atlantic molly (*P. mexicana*, ♀) about 100.000 years ago [94, 194, 197, 136, 209, 231]. This species reproduces through gynogenesis which means that females require sperm from males of closely related Poeciliid species to induce embryogenesis [65]. However, no genetic material from the male is incorporated into the embryo, allowing the Amazon molly to produce broods of offspring that are genetically identical to each other and their mothers [193]. The herein used clonal linage has been reared for many generation in captivity and regular molecular checks confirm that individuals are clones. Fish were bred with Atlantic molly males as sperm donors at the animal care facilities of Humboldt Universität zu Berlin. Fish were reared in 200-L tanks filled with aged tap water at a temperature of 26 °C and fed twice daily *ad libitum* with commercially available flake food as well as defrosted blood worms (*Chironomidae sp.*). All animal experiments were conducted under the animal experiment number

#0089/21 of the German State Office for Health and Social Affairs (LAGeSo).

Figure 1. The Amazon molly *Peocilia formosa*

2.2.2. Experimental design

For our experiment, we first generated two different treatment groups, one that was fed three times per day for one week only inside an opaque cylinder ('trained cohort', Figure 2), while the other one was fed with food dispersed randomly in the experimental tank ('naive cohort'). In a second step, we visually paired fish with individuals from the same or a differing training regime and either continued (for those already trained) or started to feed only in the cylinder (for those habituated, but naive).
To start the experiment, we placed pairs of size-matched, unfamiliar fish (N=36, 23±2 mm) in each of six identical test aquariums (300 × 600 × 200 mm). Fish were taken from multiple husbandry tanks ensuring that familiarity was not given, and size-matched in order to reduce dominance effects and most importantly to account for any age differences. All individuals were randomly distributed across all experimental tanks. An opaque divider separated each tank into two same-sized compartments, each containing one fish. This divider could be exchanged with a transparent one during experimentation to allow visual interactions (see Figure 3). Each two-compartment tank was externally filtered (EHEIM Professional 3 250) throughout the entire trial in order to maintain water quality and to provide olfactory cues to the fish. Water quality was checked weekly (SERA pH, NH_3/NH_4,NO_2,NO_3) and 50 percent of the water was exchanged at the same interval. The temperature was maintained within the range of 23-26 °C and adjusted through the ambient room temperature. Water levels were maintained at 70 mm, resulting in a total of 18.7 l per tank and 3.5 l per individual compartment. In order to enhance the learning outcome, the fish were kept on a continuous light cycle, which has been shown to have no effect on the stress level of a closely related species, while improving the learning abilities [129]. All fish were fed with frozen blood worms, which were thawed approximately 30 min. before each experiment.

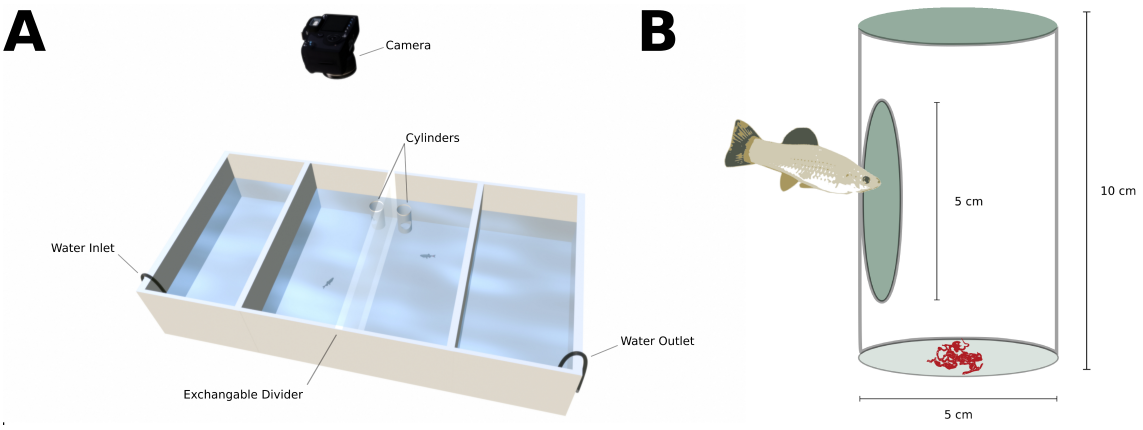

Figure 2. **A** Schematic of the general recording setup. Each inlet and outlet was attached to an individual circulating filter system. **B** Concealed food source used in the conditioning trials. Food was presented within an opaque cylinder, that could only be accessed through a horizontal opening. Entry into the cylinder was monitored through the top opening, vertically facing the camera. The cylinders were glued to ceramic plates to ensure stability. This further ensured that food particles and olfactory cues were contained within the cylinder.

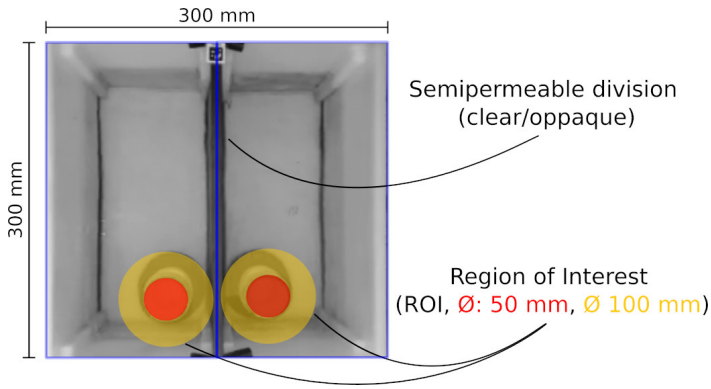

Figure 3. Top-down view of the holding tanks, showing the central most compartments, housing one individual on each side. The location at which the cylinder as food source was placed is denoted as region of interest and marked in red. The exchangeable central division, which could be either clear or opaque is shown in the middle. The position of the separator to standardize the starting distance at the beginning of each test instance is shown as green dashed line.

2.2.3. Food conditioning experiments

Individual Learning Phase - Week 1

For the individual conditioning, we randomly selected future demonstrators and observers within each of six simultaneously trained pairs. Demonstrators were then trained on six occasions per day, for at least five consecutive days without visual access to the conspecific partner. Each training instance, consisting of eight minutes, was recorded using consumer-grade webcams (c920 HD Pro Logitec, USB 3.0, 432 × 240 px, grayscale, 30 fps) mounted above each individual tank. It was ensured that the camera was centered precisely above the tank in order to keep occlusions and perspective distortion minimal and evenly distributed among both individuals being recorded. During a training instance the individual was either presented with a white opaque, vertical PVC cylinder (height: 100 mm, ⌀: 50 mm, see Figure 2), containing food as stimulus or with a mock stimulus (50:50 - mock:real). This resulted in three mock treatments and 3 actual training instances per day, for every individual. To standardize the starting distance of the fish to the food source, individuals were limited to one side of the compartment at the beginning of each instance. This was done using a small separator (see Figure 3). For mock treatments the fish underwent all steps, as if it was an actual training instance, being constrained to one side of the compartment and having this separator subsequently removed, but without the following stimulus presentation. The choice for true conditional or mock stimulus was randomized over the course of the day, while ensuring that each accounted for 50% of the total daily tests (3 true, 3 mock). Mock treatments were introduced to reduce any association with other neutral stimuli of the procedure and to ensure that the focus was drawn to the actual task being learned [52, 186, 7]. For the trained cohort of fish, the cylinder was stocked with blood worms (N≈8) which were visually occluded from the fish and only accessible through a round opening in the side of the vertically oriented cylinder (see Figure 2). Fish of the naive cohort were treated with identical conditions as their trained counterparts, with the only difference being the location at which food was presented. Here, the same amount of food was distributed randomly within the tank and accessible for the duration of the test instance. The task was found to be solved when an individual continuously spent 1 s or more inside the cylinder. At the end of each test instance the cylinder as well as any remaining food particles were removed from the tank using a pipette.

Social Learning Phase - Week 2

In the second week of the experiment, individuals were regrouped with a new size-matched partner and randomly redistributed across the six experimental tanks. This was done to ensure that each individual was relocated to a new test tank. Regarding the individual's own and the partner's initial training, the following social

treatments were created: trained paired with trained individuals (TT), naive paired with trained (NT) or trained with naive (TN) as well as naive paired with naive (NN). The previously opaque division, separating the two individuals was replaced by a clear one, enabling full visual access between both individuals (see Figure 3). This clear division was left in place for the entire duration of the social trial, which lasted for five consecutive days. During this period all individuals were being trained and tested according to the individual conditioning procedure previously described, receiving food only within the cylinder (see Figure 2).

2.2.4. Video Analysis

In order to quantify the learning outcome, fish were tracked using a custom developed tracking software implemented in Python and using the computer vision library OpenCV [31]. The fish were detected by using frame-wise motion tracking, based on simple background averaging and subsequent background subtraction. Detected objects were further filtered based on size, speed and using an isolation forest algorithm to limit detections to actual fish and reduce noise due to reflections and moving particles to an absolute minimum. Individual positions were given as two-dimensional Cartesian coordinates, calculated as the center of mass of each filtered detection contour. Since background subtraction can result in missing observations due to little movement of the animal, all coordinates were interpolated linearly over time to account for this. The first 30 s of each test instance were considered the acclimation phase, in which the animals were allowed to settle after having the separator removed. This period was exempted from further analysis. To further standardize recordings, all recordings were restricted to a maximum duration of 433 s, leading to a total duration from start to end of 403 s. Given that each individual was restricted to its specific compartment, identities were maintained based on spatial discrimination. Presence and position of the stimulus cylinder were automatically determined by using an implementation of the Hough transformation, returning the coordinates of the center of mass and the radius of the detected cylinder. This enabled the exact measurement of the Euclidean distance of each individual to the cylinder center at each given time point. In addition to the automated process, all videos were manually checked for validity of cylinder detection and tracking results.

2.2.5. Statistical analysis

All statistical analysis was run in R (v3.6.3 'Holding the Windsock') and statistical inference based on generalized mixed effects models (more specifically logit models) which were composed using the function `glmer` in library `lme4` (v1.1-32). After tailoring models to the experiment and research questions, further model selection was done based on Akaike's information criterion (AIC) or conditional AIC,

where applicable, using the library `cAIC4` (v1.0) and `AICcmodavg` (v2.3-1). Validation and estimation of accuracy was done using the `check_model` function in the `performance` library (v0.10.3). Test statistics and summary calculations were done using `tab_model` in the library `sjPlot` (v2.8.14). For testing variance components, we use the boundary correction described by Stram and Lee [211] for linear mixed effect models. Significance is reported on a 95%-level and all confidence intervals (CIs) provided are given as 95% CIs.
Individuals $i = 1, \ldots, 36$, equipped with universal unique identifiers (UUIDs), are defined to have reached the region of interest (i.e. solved the task) in test instance $j = 1, \ldots, 15$ (response $y_{ij} = 1$) if their distance to the cylinder center was smaller than 2.5 cm over a duration of 1 s or more, and to fail otherwise ($y_{ij} = 0$). Predicting that fish should increase the likelihood to solve the task when being fed within the cylinder, we associate the learning performance of individual i with its probability of reaching the region of interest and employ a statistical learning model based on logit regression reflecting each of our main hypotheses in a single model coefficient. Two slightly different model variants are used for experiments of Week 1 (Model 1) and Week 2 (Model 2). Model 1, addressing questions of private information acquisition, is given by

$$\log \textsc{odds}_{ij} = A_i + B_i\, t_{ij} = \alpha_0 + \alpha_1 x_{\mathrm{T}i} + a_i + \big(\beta_0 + (\beta_1 + b_i)\, x_{\mathrm{T}i}\big)\, t_{ij} \tag{2.1}$$

where probabilities P_{ij} of success $y_{ij} = 1$ are modelled via odds $\textsc{odds}_{ij} = \frac{P_{ij}}{1-P_{ij}}$ of 'expected # solved : expected # failed', allowing for interpretation via odds ratios (OR). The combined intercept A_i determines the baseline odds of reaching the region of interest. This corresponds to the baseline likelihood of an individual reaching the region of interest, before having any prior experience on entering it (Test Instances 1-2, illustrated in Figure 4). The slope B_i reflects the learning rate of individual i, with $\textsc{odds}_{ij}$ expected to increase with the number of visits t_{ij} after initially solving the task (count variable, Time since solved ≤ 15, illustrated in Figure 4). For the probability p_{ij} of solving the task, this results in a sigmoidal learning curve in t_{ij} (Figure 6). With $x_{\mathrm{T}i} = 1$ if individual i is trained and 0 otherwise dummy-coding the training status, $B_i = \beta_0 + (\beta_1 + b_i)\, x_{\mathrm{T}i}$ is composed of a reference slope β_0 reflecting the learning behaviour of un-trained individuals and the gain in the learning rate β_1 for trained individuals as fixed effects, plus a random effect b_i reflecting subject-specific deviations of trained individuals. This applies analogously for A_i as well. The random effects a_i and b_i are assumed normally distributed with standard deviations τ_a and τ_b, respectively, and correlation ρ. The random slope b_i is restricted to trained individuals, which are of major interest. In this model, $\beta_1 > 0$ corresponds to Hypothesis I that clonal fish are capable of learning to feed inside the provided cylinder, in that it reflects deviation from zero in the learning rate, and $\tau_b > 0$ corresponds to Hypothesis II that learning behaviour is subject

specific, as it describes the variation among individual learning abilities. Including an indicator $x_{\text{solved}\,ij}$ as additional covariate into Model 2.1, which is 1 if the ith individual has reached the region of interest before the jth training instance and 0 otherwise, has been considered to enable less gradual learning behaviour but turned out unfavorable in AIC-based model selection.
Model 2, designed for comparing learning behaviour of individuals in pairs with different training history, is given by

$$\begin{aligned}\log \text{ODDS}_{ij} = A_i + B_i\, t_{ij} &= \alpha_0 + \alpha_1 x_{\text{NT}i} + \alpha_2 1_{\text{TN}}(i) + \alpha_3 x_{\text{TT}i} + a_i \\ &\quad + (\beta_0 + \beta_1 x_{\text{NT}i} + \beta_2 x_{\text{TN}i} + \beta_3 x_{\text{TT}i} + b_i)\, t_{ij}\end{aligned} \tag{2.2}$$

where $x_{\text{NT}i} = 1$ if individual i is in group NT, i.e. was not trained in Week 1 but has an experienced partner, and 0 otherwise. Analogously for TN and TT. Accordingly, β_0 describes the baseline learning rate in reference group NN and $\beta_1, \beta_2, \beta_3$ reflect the deviation from that in the other treatment groups. In particular, $\beta_1 \neq 0$ indicates differences in learning behaviour of naive fish with trained partners (Hypothesis III). Random effects a_i and b_i are specified analogously to Model 2.1 to account for subject-specific variations.

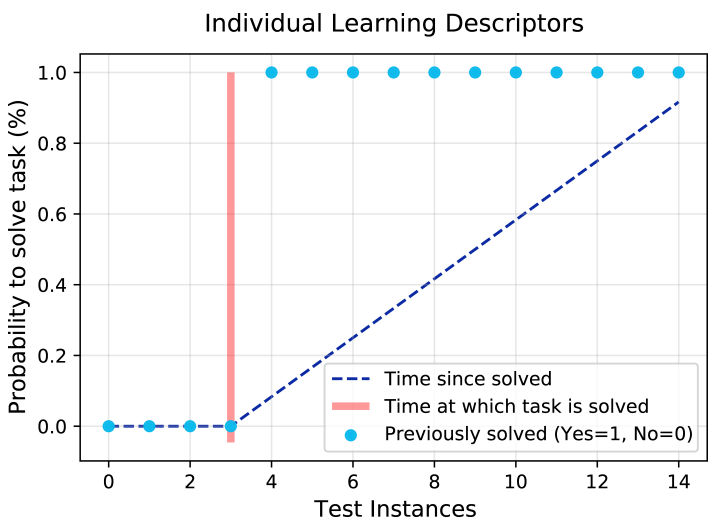

Figure 4. Definition of the 'time since solved' t_{ij} used as variable for individually describing the learning process. Until the food inside of the cylinder was first found by individual i at test instance $J_i = \min\{j : y_{ij} = 1\}$, no training effect can occur and $t_{ij} = 0$ for $j < J_i$. After that, individual training commences and training time monotonically increases as $t_{ij} = j - J_i$.

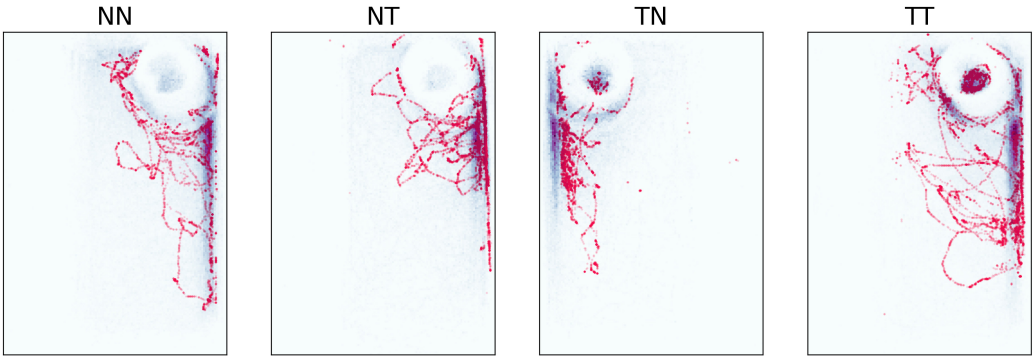

Figure 5. Overview of space use across treatment groups in the second week of training (order from left to right: NN, NT, TN, TT). Only instances where the cylinder was present are shown. Darker coloration represents higher number of occurrences, lighter lower. Sample trajectories are shown for random individuals of each treatment group. All trajectories where centered on the cylinder, for better visualization.

2.3. Results

2.3.1. Amazon mollies are able to quickly learn foraging task

Our first question was whether clonal fish were capable of learning to feed inside the provided cylinder. We verify this based on Model 2.1, which captured the variance within the data well, while random effects accounted for a large proportion of the variance (marginal R^2: 0.830, conditional R^2: 0.839, following Nakagawa et al. [162]) (see Supplemental Material Table 3). At baseline, we obtain odds of about 1 : 9 (probability $P_{ij} = 0.10$) for an untrained fish to reach the region of interest within a test instance (given by intercept $\alpha_0 = -2.18$, CI = $[-2.80, -1.57]$, for $b_i = 0$). This corresponds to the probability of an individual to enter the region of interest without having ever entered it before (see Figure 4: Test Instance 0-2). For individuals being trained, and thus not being fed outside the region of interest, we obtain a slightly higher baseline probability, with the odds increased by a factor of $\exp(\alpha_1) = 1.55$ (CI = $[0.67, 3.56]$, p=0.302), which is, however, not significantly different to those not being trained. While we even observe a slightly negative 'learning effect' of entering the cylinder ($\beta_0 = -0.14$, CI = $[-0.35, 0.065]$, not significant) for individuals not being trained, a significant positive learning effect is obtained for trained individuals ($\beta_1 = 1.37$, CI = $[0.60, 2.14]$, p<0.001 ***). The likelihood of trained individuals to reach the food source significantly increased, once they had solved the task for the first time (see Figure 4: Test Instances > 3), with an odds ratio of OR = $\exp(\beta_0 + \beta_1) = 3.42$, CI = $[1.60, 7.30]$ more than tripling the odds for the next visit (in a conditional ceteris paribus interpretation used also in the following). Figure 6 depicts estimated mean learning curves with and without training, showing probabilities P_{ij} of solving the

task in dependence on t_{ij}, and illustrates how the time spent by fish in the region of interest increases with t_{ij}.

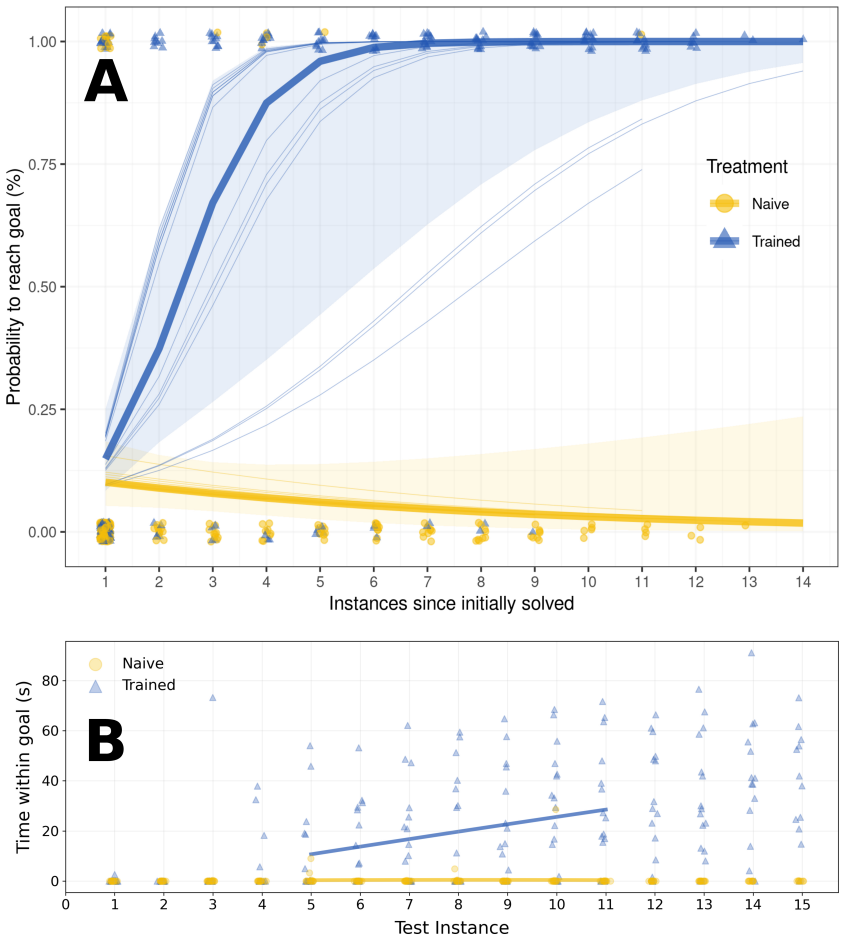

Figure 6. Learning outcome of the two treatment groups (trained/naive) in the first week. Both graphs show results from 36 individuals: Naive: N=18, Trained: N=18. **A**: Model output the first week of training in form of estimated marginal means (lines, thin: individual; bold: group mean) and raw data (points). Instances along the x-axis are in respect to the first time the goal was reached. Confidence intervals are based on the Upper Control Limit (UCL) and the Lower Control Limit (LCL) at a 95% confidence level. **B**: Visualization of time spend within goal area across both treatment groups (trained/naive) and over all test instances in the first week. A truncated linear fit is shown as trend line (between instance 5-11), estimated over all data points and for each treatment group. A slight jitter was applied along x in order to reduce overlap.

2.3.2. Clonal Amazon mollies individually differ in learning ability

We approached the question, whether individual variability was observable among the learning abilities, and more specifically the probability to reach the goal area, using the same model as in I (Equation (2.1)) by investigating the random effect b_i on the learning rate of trained individuals. A standard deviation of $\tau_b = 0.74$ is estimated for b_i which bespeaks considerable variation across individuals accounting for about $\tau_b/(\beta_0 + \beta_1) = 60\%$ of their mean learning rate, and testing for $\tau_b > 0$ confirms significant inter-individual differences in the learning behaviour (p<0.001 ***). Aside of differences in the learning rate, the standard deviation $\tau_a = 0.43$ of the random intercepts a_i could be interpreted to reflect differences in the exploration behaviour of individual fish. It is, however, not significantly > 0 (p=0.386). Inter-individual differences are also supported in terms of model selection, preferring Model 2.1 with random effects (marginal AIC = 314, condictional cAIC = 259) over an analogous model without random effects (AIC = 342).

2.3.3. Social effects of informed partner can hinder own learning

The pairwise interactions in the second week, allowed to assess whether task performance was worse in observers paired with naive demonstrators, compared to those interacting with task-proficient ones. For this purpose we refer to results of Model 2.2, which are also illustrated in Fig. 7 A. Overall the model (see Model 2.2) to determine these effects captured the variance within the data well (marginal R^2: 0.716, conditional R^2: 0.903) (see Supplemental Material Table 4). In Week 2, naive individuals showed similar baseline probabilities for initially entering the region of interest when paired with naive partners as they did in Week 1 (reference group NN: odds $\exp(\alpha_0) = 0.07$, CI = $[0.02, 0.25]$). The baseline probabilities are substantially increased for experienced individuals (TN vs. NN: OR = $\exp(\alpha_1) = 24.74$, CI = $[2.82, 216.76]$, p=0.004 **) in accordance with the training effect affirmed above. However, there was no evidence for a positive effect of the partner's experience on own probability of initially entering the cylinder. By contrast, our data indicates a negative effect of having an experienced partner on both naive and trained individuals (NT vs. NN: $OR = \exp(\alpha_1) = 0.39$, CI = $[0.04, 4.04]$, p=0.432; TT vs. TN: $OR = \exp(\alpha_3 - \alpha_2) = 0.92$, CI = $[0.10, 7.79]$, p=0.938) which is smaller for the trained: the odds to initially reach the goal area were decreased by $\sim 61\%$ in naive individuals, when paired with an informed individual. For already trained individuals paired with another trained partner this effect was smaller, amounting for a 8% decrease. Although these effects on the initial detection probability are subject to considerable estimation uncertainty and not significant, a significant negative effect of the partner's experience on the learning rate (reference NN: $\beta_0 = 2.03$, CI = $[1.14, 2.92]$) is found for naive individuals ($\beta_1 = -1.77$, CI = $[-2.99, -0.56]$,

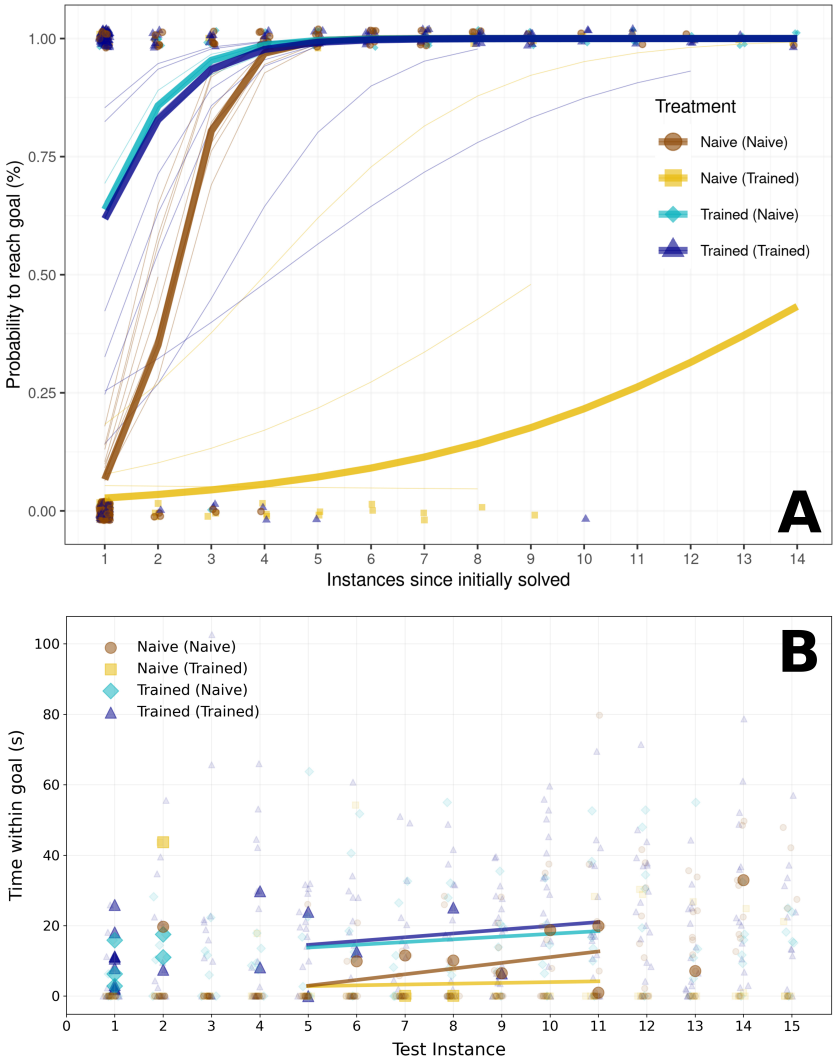

Figure 7. Learning outcomes of four treatment groups, depending on the focal individual and partner denoted in brackets: Naive (Naive): $N = 12$, Naive (Trained): $N = 6$, Trained (Naive): $N = 6$, Trained (Trained): $N = 12$. **A**: Model output the second week of training in a social context. Results are shown in form of estimated marginal means (lines, thin: individual; bold: group mean) and raw data (points). Instances along the x-axis are in respect to the first time the goal was reached. **B**: Visualization of time spent withing goal area across all treatment groups and over all test instances in the second week. For better visibility, first solved instances are shown with large icons and higher contrast. All remaining data is shown with less contrast. A truncated linear fit is shown as trend line (between instance 5-11), estimated over all data points, for each treatment group independently. In order to reduce overlap in the plot a slight jitter was applied to the data.

p=0.004 **). For NT vs. NN, the probability for reentering the region of interest after the first visit is, hence, significantly reduced with an odds ratio of $OR = 0.17$ (CI = $[0.05, 0.57]$), when paired with a experienced social partner. For experienced individuals, the negative effect of having an experienced partner is less distinctly expressed, yielding $OR = 0.87$ (CI = $[0.20, 3.64]$, p=0.847, not significant) for TT vs. TN. In our experimental setup, we thus consistently find performance decreased for individuals with experienced partners when comparing them to individuals with naive partners – an effect that is significant, however, only for the learning rate of naive individuals with experienced partners, where it is also most pronounced.

2.4. Discussion

In the present study, we found that clonal Amazon mollies can be trained according to a classical operant conditioning task, that they exhibited among-inter-individual differences in their learning performance, and that the presence of a task-experienced social partner reduces own learning and task-solving performance, especially for task-naive individuals.

Clonal Amazon mollies can learn in an operant conditioning paradigm within a few days and a low number of repeated training sessions to associate food with a location in their laboratory environments. This is in line with current research on fish cognition, which shows that fish are avid learners and have sophisticated cognitive abilities [35, 124, 40, 24]. Further, Fuss and Witte [71] and Fuss et al. [70] found similar learning capabilities in both parental species of the Amazon molly, *P. latipinna* and *P. mexicana*, and also in the closely related guppy (*P. reticulata*). It was shown that both mollies and guppies are capable of operant conditioning as well as reversal learning, thus it is not surprising that we found similar cognitive capabilities in the clonal Amazon molly. Our results suggest consistent individual variation in the learning curves during the solitary phase of the experiment. There is substantial knowledge about consistent individual differences in behavioural traits [184], including clonal animals like Amazon mollies [196, 67, 26]. However, learning as an individual trait has only recently been shown in great detail in the fruit fly *D. melanogaster* [204]. Here, we show that this individuality in learning can also be found in a naturally-occurring clonal vertebrate.

Eager learning can be seen as an adaptation, allowing individuals to respond to environmental changes and unforeseen circumstances. Why even genetically-identical individuals differ in their learning performance may have multiple reasons, including pre-birth processes like epigenetics differences, maternal effects [114] and developmental stochasticity [92], and may be due to post-birth processes like differences in previous experience [119] and encountered, environmental conditions [67, 5]. In the here presented study all individuals were genetically identical and

reared under near identical conditions. However, we used individuals from different mothers and individual variability among our test subjects can thus be due to a variety of these variance-inducing processes [26]. Further experimentation is needed in order to point out which factors are the most prominent drivers of among-individual variation in the learning performance of this clonal vertebrate species.

As shown here, the skill level and performance of a social partner indeed has a strong influence on own performance but in an unexpected way. We found that naive individuals paired with trained ones exhibited slowest learning, when compared to naive individuals paired with other naive ones. Trained individuals that were associated with naive partners did not significantly differ from trained individuals that were paired with other trained ones, although our results tend towards hindering, rather than supportive effects of observing trained partners. Therefore, it seems as though being accompanied by highly skilled conspecifics did not improve own learning performance, and that having a naive social partner was more beneficial during learning, when being naive to the task as well. So, how can such counter-intuitive effects be explained?

First, the goal areas of both social partners were in mirrored locations (see Figure 3), such that the behaviour of the other would not necessarily lead to the same information, visual cues and ultimate learning outcome. Trained individuals have acquired experience and established a procedure of solving the task. This can manifest in behaviours such as accessing the goal from a certain direction, location or at a specific time, which in turn do not necessarily match those of the social partner leading to a dissonance between observed and performed behaviour. For two naive individuals performing the task together this could not have such an impact, since both individuals are acquiring the knowledge about the novel task at the same time, leading to more synchronous experience between both individuals. Following the logic that naive social partners simultaneously learning the task from initial non-proficiency show more undirected and variable behaviour, Kohn [125] argued that a continued perception of change, as would be the case when watching another naive individual trying to perform a novel task, can maintain attention and act reinforcing to the observer. The experienced partner would merely repeat its already learnt behaviour and result in less variation and subsequent reinforcement for the naive observer.

Second, our task was designed in a way that the observer did not see the demonstrator actually feed. In studies that found local or stimulus enhancement effects [36], observers could actually see demonstrators getting the benefit and we argue that a lack of seeing the direct benefit in our study hampered the social learning especially from experienced demonstrators that virtually disappeared when performing the task. This is underpinned by the fact that trained partners have little effect on initially reaching the cylinder and food source in their naive social partners, where we only observe a smaller, non-significant effect. However, the detrimental effect of having an

experienced partner is clearly pronounced in the chance to subsequently re-visit the region of interest in the naive individuals, where we observe a strong and significant decrease in their learning rate. This indicates a more complex effect than pure spatial misguidance, due to mere copying and also rules out positive effects such as stimulus enhancement [207] or local enhancement [220] due to the trained demonstrator.

2.5. Conclusion

In congruence with our results, weak or absent positive effects of highly skilled partners have been found in studies using full-contact designs during demonstrator-observer interaction and path learning tasks. In the guppy, naive individuals were following familiar, but less skilled partners more readily through unknown maze setups [214]. Similarly, in zebrafish food income equality was enforced via social information, where observers relied on visual, behavioural cues of successful demonstrators to find food themselves [191]. In pigeons, Biederman and Vanayan [23] showed that naive individuals observing demonstrators performing a task at chance and gradually improving, outcompeted those observing well proficient demonstrators in speed of learning and overall task accuracy. Further, although near identical and clonal, our tested individuals show consistent differences in their learning behaviour which is in line with previous studies proposing consitent among-individual differences being common also in clonal animals [196, 26, 67] In sum, this study builds upon the well established field of operant learning and conditioning, utilizing a naturally clonal fish species as model organism, in which learning has not yet be studied. The here presented work adds a sleek and interpretable approach to analysing both the learning efficiency, as well as the inter-individual differences in the learning performance. This is done by carefully constructing a statistical model, along side the experimental design, in which all components represent key aspects of interest, and biologically relevant terms such as learning rate and overall exploration. The here highlighted insight, that prior knowledge, or information contained within one's social partners has an effect on the own performance in certain contexts has broad implications for collective behaviour and group performance. It has already been shown that information differences can explain dynamics within animal collectives [100, 146]. Information quality [111], such as uncertainty and redundancy, as well as the processes by which novel information is generated or affected by the social environment most likely play a key role in the learning behaviour of gregarious individuals [91, 187]. In light of learning - a process of information uptake and integration over time - the here presented results give a concise approach to shed light on the timing of such events. The process of learning and timing of informational cues gives rise to a multitude of interesting questions, such as how information is being distributed in a multi agent system, or fish school, in order to achieve optimal

exposure and learning for each of its individual members.
In more biological terms, what drives an individual to take on a certain role in the group, move to a specific location or perform a given behaviour is still very much an open question, which yearns to be answered. As shown here, the experience and prior knowledge of social partners has an effect on the learning performance of individuals. Therefore, the social environment during certain experiences likely effects the ability of individuals to learn and adapt to novel situations. These insights, as well as the unique modelling approach shown here to address such learning processes and their timing, should pave the way for more experiments in this exciting direction.

3. Jumping as a Socially Mediated Behavior

As the previous work highlighted, behavior is affected by the presence and actions of others. This was based on the experimental conditioning of single individuals and pairs. In the following, we focused on the social contagion of behavior in larger groups of individuals. To do so, instantaneous behavior which clearly can be seen as the result of an individuals' decision was investigated. A behavior fish exhibit and which is readily observed during experiments, often to the discomfort of the experimentor, is the jumping behavior. In the case of a jump the fish launches itself vertically from the water and into the air. The reliability of such behavior in a laboratory setting was used, to test contagion of such behavior and the associated decision in a social context.

3.1. Introduction

In gregarious animals, group members readily synchronize their behaviours and often respond quickly to their neighbors' actions [127]. As a consequence of this coordination, a cascading spread of information (e.g., in the form of behavioral state changes) can be observed, for example when single individuals perform evasive movements that are then adopted by neighbors leading to wave-like phenomena running through large parts of the group. These phenomena have been intensively studied in shoaling fish, as they often readily show anti-predatory behavioral responses [190, 59, 206, 121, 106, 60, 178]. The degree to which individuals adopt and copy behavioral decisions of neighboring individuals may well depend on the social context. For example, guppies (*Poecilia reticulata*) follow familiar conspecifics more readily into unknown areas, compared to unfamiliar ones [214]. Further, young guppies copy mate choice decisions from older, more experienced individuals but not vice versa [62]. In addition, other social factors like size of the group (group density) or perceived or actual risk of predation can affect quantity and quality of social contagion phenomena [206, 121, 178]. So, for a mechanistic, as well as functional understanding of social contagion processes, we still need to understand how and which social factors may influence the decision to adopt behavioral changes from neighboring conspecifics. Here we focus on the influence of social factors (familiarity as well as group size) on an individuals' tendency to adopt conspecifc decisions using a highly social all-female fish species, the clonal Amazon molly (*Poecilia formosa*). We make use of the fact that this species, as many other fish species, occasionally jumps out of the water. Fish may do so in order to leave unsuitable habitats [11, 195] or escape attacking predators [16]. These jumps, similar to evasive fast-starts [190],

occur spontaneously without a triggering, external stimuli, and therefore allow us to investigate (a) whether the familiarity towards a jumping conspecific facilitates the own decision to jump (as would be predicted by leader-follower experiments of Swaney et al. [214] and Reader et al. [183]) and (b) whether the number of conspecifs in the group increases the likelihood of initiating and copying the jumping decisions [244, 236]. Specifically, we asked whether fish would jump more readily when paired with a known, familiar conspecific partner as compared to when paired with an unknown, unfamiliar partner. Using the clonal Amazon mollies, a naturally occurring clonal *Poeciliid* species, for our experiments, we reduced effects of sex and genetic differences that may affect the tendency to copy and follow a conspecific. This species is highly social and individuals are able to familiarize with conspecifics when reared together [149, 59] . Specifically, we predicted that the likelihood that at least one individual out of a familiar pair jumps into the unknown is higher than in the unfamiliar pairs and that if one individual jumps the likelihood that the other one jumps is also increased. To test these predictions, we observed the individual likelihood to jump when familiar and unfamiliar pairs were transferred into small bowls, from which they could only escape by jumping into the unknown outer area of the tank. In a second experiment, we asked whether jumping decisions of single individuals can influence their neighbors' likelihood to jump, leading to cascade-like collective jumping. Here, group size may play a role which is why we observed groups of varying sizes in a large tank and extracted time and location of evasive jumps. By modelling the influence of a previous jumping event on the probability to jump in the next time step, we explored whether found patterns point towards socially induced decisions for jumping thus social facilitation of a life-and-death decision.

3.1.1. Jumping behaviour in fishes

The peculiarities of fish jumping was already described in 1951 by Aronson et al. [11], who made early observation of frillfin gobies (*Bathygobius soporator*) jumping from one tide pool to another. Since then, besides studies on the kinematic mechanisms [78, 205, 39] and a recent approach by De Waele et al. [58], jumps have sparsely been explored. This is peculiar, since the stakes are high and an individual's decision to jump out of the water is a decision of life-and-death as the final destination of the jump is often uncertain or unknown. Mobile animals are able to actively choose their habitats to some extent and thus move towards places where environmental conditions are favourable for their homeostasis [50]. When conditions become unsuitable in one habitat, animals often switch to more favorable habitats and this is relatively easy for terrestrial or aerial species. For those species bound to the aquatic realms, movement between habitats is often more constrained. Some fish, the Snakehead murrel (*Channa striata*) and some members of the air-breathing catfish

family (*Clarias*) for example have adapted to walk over land [130], but others such as the zebra fish (*Danio rerio*) and the killifish (*Gambusia affinis*), use terrestrial jumps as escape response [78]. The Trinidadian guppy (*Poecilia reticulata*), a well studied member of the genus *Poecilia*, has also been shown to perform such evasive jumps [205]. Further, De Waele et al. [58] showed that guppies are capable of incorporating information to direct their jumps towards safe locations.

3.2. Methods

3.2.1. Animal maintenance

All animal experiments were conducted under the animal experiment number #0089/21 of the German State Office for Health and Social Affairs (LAGeSo). Experimental fish (strain PfII_1304) were kept and bred in the laboratories at HU Berlin over successive generations. Fish were housed in 34.1 L communal aquaria, which were part of a 400 L recirculating system. All holding tanks were maintained at 24 °C and water values were tested weekly (SERA test drops) to assure optimal water quality (8.11 pH, 14.67 GH, 8.67 KH, 0.02 NO_2 mg/L, 17.33 NO_3 mg/L, < 0.05 NH_4 mg/L, 0.62 PO_4 mg/L, 2.96 mS/cm Conductivity). To mimic natural diurnal patterns all animals were kept on a 12:12 hour light-dark cycle. Fish were fed a variety of dry flake food, live bloodworms (*Glycera sp.*) and *Artemia sp.* three times a day (0930, 1400, 1600).

3.2.2. Experiment I: Pairs

In order to investigate the effect of familiarity of the group members on an individuals' decisions to jump into an unknown environment, we created pairs of adult Amazon mollies that were either kept together since birth (familiar) or fully unknown to each other (non-familiar). These pairs were transferred into a water filled bowl (diameter: 14 cm⌀, Ceramic, 5 cm water level) that was placed into a larger tank (diameter: 120 cm⌀, PVC) with a slightly lower water level, but otherwise identical conditions. We simultaneously observed 10 pairs (5 familiar, 5 non-familiar) for 90 minutes and repeated this setup 4 times to reach a total sample-size of 20 familiar and 20 non-familiar pairs (Total number of individuals: N-familiar=40, N-unfamiliar=40). Body size (total length) was measured from still images and treatment groups did not differ significantly (familiar: 34.2 mm, non-familiar 32.8 mm; t-test: t78=1.686, p=0.096). During the observation period, the tank was vertically filmed from above using a high resolution camera (Basler acA2040-90umNIR, 2048×2048 px, gray-scale, 25 fps) and by using the Motif video recording software (loopbio GmbH, Vienna, Austria). From the videos, the time point at which a fish jumped out of the bowl

into the outer compartment of the tank as well as the distance of the jump were extracted. After the observation period all fish were transferred back into their respective holding tanks and were not subject to any further experimentation.
To answer the question whether individuals with a familiar partner were more likely to jump compared to those with an unfamiliar partner, we first compared the number of pairs in which at least one individual jumped between familiar and non-familiar treatments using chi^2 tests. Subsequently, we compared the number of pairs for which both individuals jumped to the cases where none or only one fish was jumping between treatments (chi^2 tests). Using the time until a fish jumped out as dependent variable, we further compared treatments via a survival analysis (cox regression) including average body size in a pair as well as body size difference as covariates. Individuals that did not jump until the end of the observation period were censored. Furthermore, we compared individual jump distance between treatments using a linear regression with average body size as well as body size difference as covariates.

3.2.3. Experiment II: Groups

In order to ensure sufficient randomization all fish were caught from the holding tanks prior the experiments and separated into individual containers. Once all individuals were captured they were each randomly assigned to one of the designated groups of varying sizes (N = 4, 8, 16, 32). Once groups were created these were allowed to familiarize for one week, before testing. In total two separate, yet methodologically identical runs were performed resulting in N=8 groups (2×N=4, 2×N=8, 2×16, 2×32) and 16 recordings. However, to limit the number of total fish required, individuals from the previous groups (run 1) were randomly recombined into new groups in the second run. Two individuals had to be replaced with naive fish from the stock between run 1 and run 2 because two fish had died between runs. During pilot studies it was established that over the course of 60 minutes individuals began to initiate jumping behaviour directed towards the outer boundaries of their tanks. This was therefore chosen as the sufficient time frame for all further recordings of this study.
Every group was then recorded twice in a white, opaque, circular arena (height: 80 cm, diameter: 76 cm⌀, PVC) for a total of 65 minutes. This was done using a high resolution camera (Basler acA5472-17um, 3672×3672 px, grayscale, 15 fps), which was installed vertically above the tank (1 m) and using the Motif video recording software (loopbio GmbH, Vienna, Austria). Consecutive recordings for each run were done on two separate days. Water levels were kept at 7 cm to reduce overlap among individuals and limit movement to the optimal focal depth of the camera. Between recordings the water was replaced with fresh, acclimatized water to ensure aeration and reduce contamination of olfactory cues and excrements.

3.2.4. Analysis

In order to quantify jumping events in larger groups, all individuals were detected and tracked over time using freely available and open source software [230]. By using a custom implementation of the Hough transformation [86, 102], designed to find circular structures, the outer, circular boundary of the tank, given by the water level on the surrounding walls was automatically detected. This allowed for jumps to be quantified as detections outside of the returned boundary circumference. These values were compared to manual annotations of frames in which jumps took place, as ground truth approach. The spatial pattern of such jumps was recorded by determining the angle of the line connecting the center of the arena and the corresponding jump location coordinates. This resulted in angular distributions around the arena center for each recording, where 0°/360° denotes due north and 180° denotes due south. The spatial distance between two consecutive jumps was calculated as angular difference. Given that the arena had a diameter of 76 cm, one degree angular change corresponds to 1.33 cm of the circular arc along the arena boundary. Further, the temporal distribution of jumps was given by time points at which jumps were detected, resulting in a fully resolved spatio-temporal distribution of jumping events across all groups.

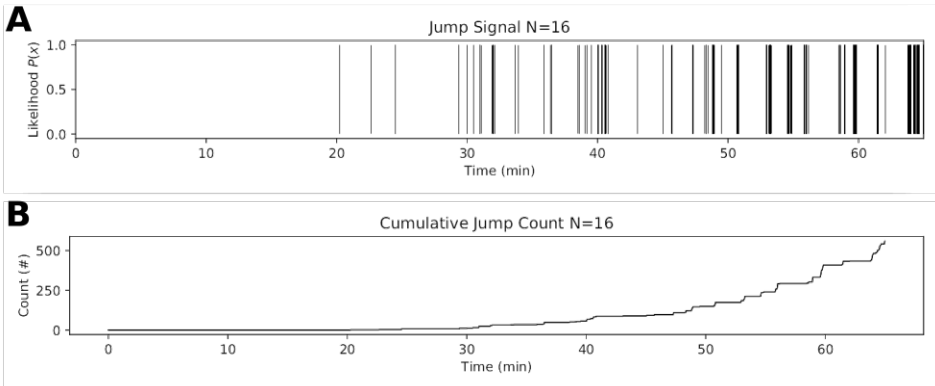

Figure 8. Example time series of jump detections over the course of 60 min for a group of N=16 individuals. **A** Time points at which jumps occurred, **B** Cumulative counts of jump events over time

Given that each group size (N=2,4,8,16,32) would likely elicit different spatial and temporal jumping patterns, comparison was done by comparing the time differences (inter-jump intervals) between jumps to those derived from randomly shuffled time series (see Figure 10). Random shuffling breaks any temporal correlation between jumps and therefore gives a good null model to begin with. Random shuffling was done by drawing the same number of observations (frames) as seen in the real data, from a binomial distribution with probability of success $P(jump)$, where the probability rate of jumping is given as:

$$P(jump) = \frac{N_{jumps}}{N_{obversations}} \tag{3.1}$$

3.3. Results

3.3.1. Experiment I: Pairs

Overall, from 40 investigated pairs observed for 90 minutes each, there were 33 where at least one individual jumped and the likelihood that at least one individual jumped did not differ between familiar (4/16) and non-familiar 3/17; chi²-test: 0.17, p=0.67) pairs. However, pairs consisting of non-familiar fish had a significantly increased likelihood for both individuals to jump out of the bowl (both jumped familiar treatment: 5/20 pairs; both jumped non-familiar treatment: 12/20 pairs, chi²=5.01, p=0.025, Figure 9A). Thus, there were overall more fish jumping in the non-familiar treatment (29 vs 21) which is reflected also in a significant effect of the factor treatment in the cox regression (treatment: chi²: 5.26, p=0.022, Figure 9B). Interestingly, most jumps (48/50) occurred within the first hour of observation (Figure 9B). The distance of a jump was not affected by the treatment (LM: $F_{1,46}$=0.791, p=0.38, Figure 9C) and body size neither affected the likelihood to jump (avg. body size: chi²: 2.631, p=0.105; size difference: chi²: 2.311, p=0.128) nor the distance jumped (avg. body size: $F_{1,46}$=0.008, p=0.93; size difference: $F_{1,46}$=0.264, p=0.61).

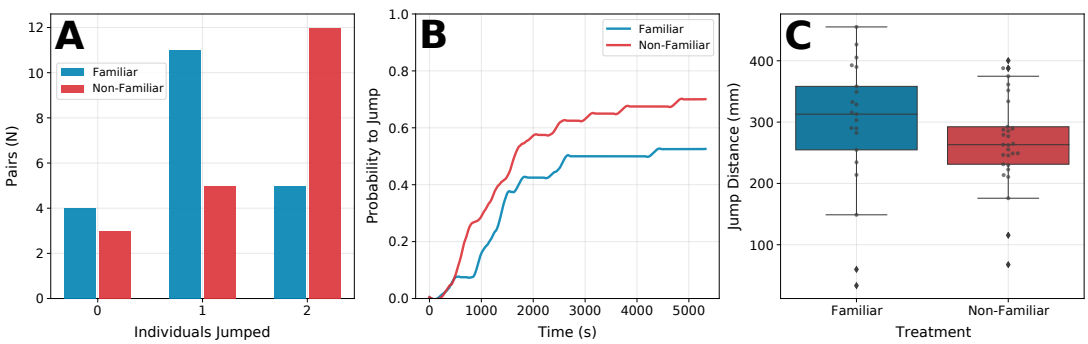

Figure 9. A Proportion of pairs in which no, one or both individuals jumped **B** Cumulative probability of an individual to jump over time and across treatments **C** Distance of jumps performed in each treatment

3.3.2. Experiment II: Groups

The individual probability to jump increased with time in the experiment (odds ratio: OR = exp(frame) = 1.46, CI = [1.35, 1.58], p<0.001 ***), group size (odds ratio: OR = exp(n) = 9.35, CI = [1.61, 54.50], p=0.014 ***) and local fish density (odds ratio: OR = exp(NND) = 1.51, CI = [1.35, 1.68], p<0.001 ***). The analysis of the time

intervals and locations between jumps revealed that jumps in all four investigated group sizes were clustered both temporally as well as spatially. The time intervals between two consecutive jumps were significantly smaller than expected from a random jump occurrence in all tested groups (see Figure 10A, Kolmogorov-Smirnov N_4: D=0.6, p=0.052 .; N_8: D=0.25, p=0.002 **; N_{16}: D=0.36, p<0.001 ***, N_{32}: D=0.37, p<0.001 ***). Similarly, the spatial distance between two consecutive jumps was significantly smaller than expected for random jumps (see Figure 10B, Kolmogorov-Smirnov N_4: D=0.55, p=0.075 .; N_8: D=0.52, p<0.001 ***; N_{16}: D=0.55, p<0.001 ***, N_{32}: D=0.37, p<0.001 ***). For both intervals and spatial distance, coefficients of distribution above 1 were calculated which are indicative of a clustered occurrence of jumps in space and time. These results indicate that fish synchronized their jumps upon each other both in time and space.

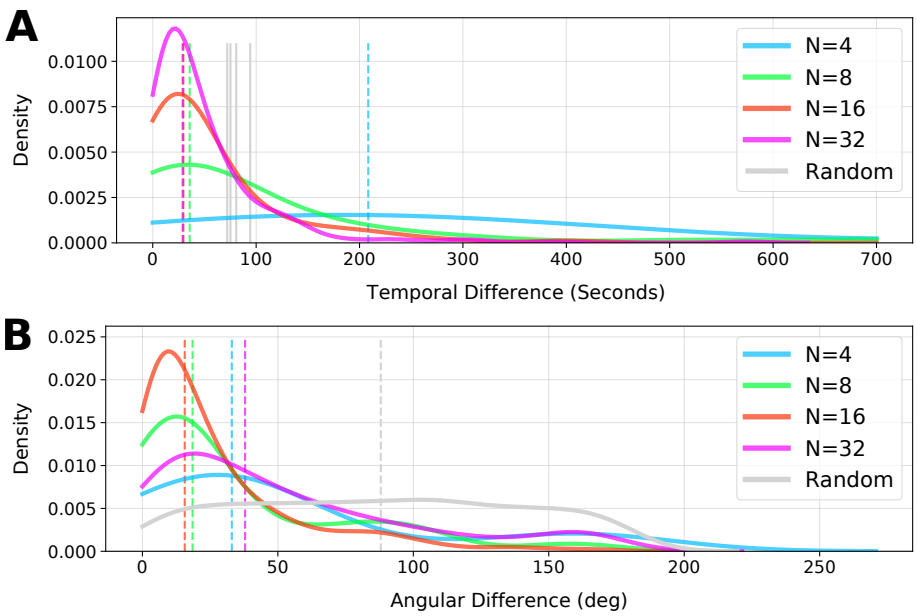

Figure 10. A Kernel density estimate of the temporal difference between consecutive jumps. Medians are shown as vertical, dashed lines and color denotes group size. Random estimates were established by sampling the same number of jumps per recording across the total time duration and calculating the corresponding interval lengths **B** Kernel density estimate of the angular difference between consecutive jumps. Random samples were drawn from a uniform distribution centered at 0 with limits -180 and 180. The number of random samples was matched to the total number of observed jumps across all group sizes.

3.4. Discussion

The here presented work shows how familiarity of social partners alters the decision-making process and risk taking in the Amazon mollies. Individuals paired with

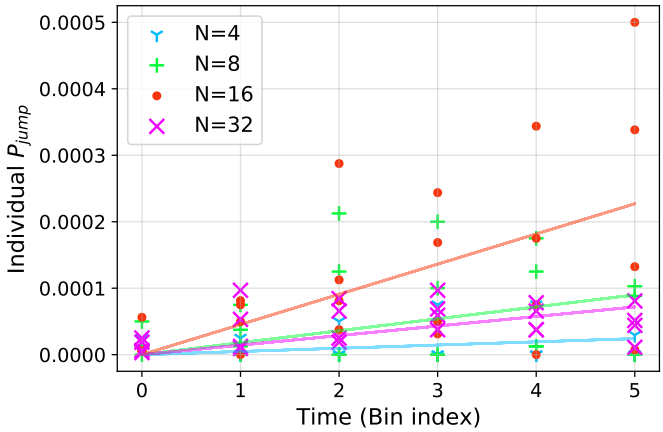

Figure 11. Correlation between time and individual jumping probability P_{jump}. The time series was split into six equally sized bins, over which the individual probability was calculated.

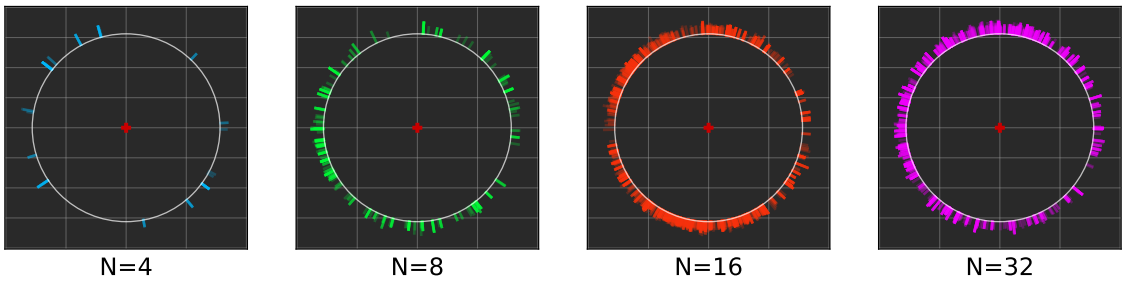

Figure 12. All detected jumps and the automatically detected arena boundaries. Length of the colored lines corresponds to relative distance of jumps. Coordinates were centered to the corresponding arena centers.

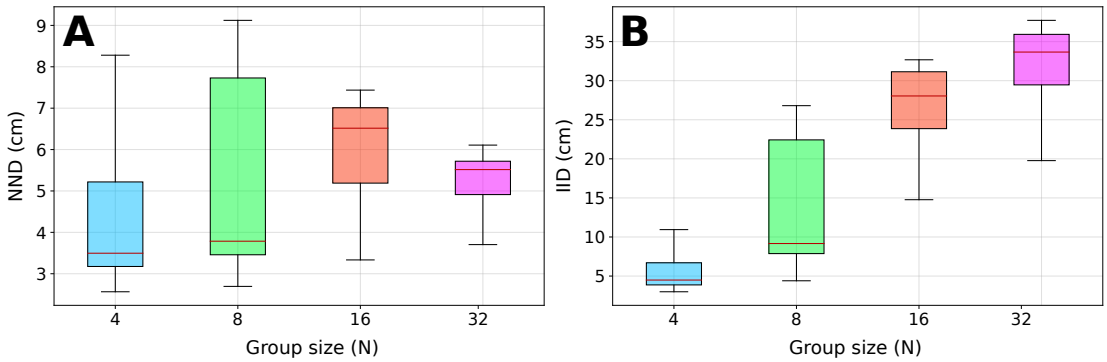

Figure 13. Boxplots showing the **A** Nearest-Neighbor distance (NND) and **B** Inter-individual distance (IID) measured between all group members in intervals of 1 s across the total duration of the recordings

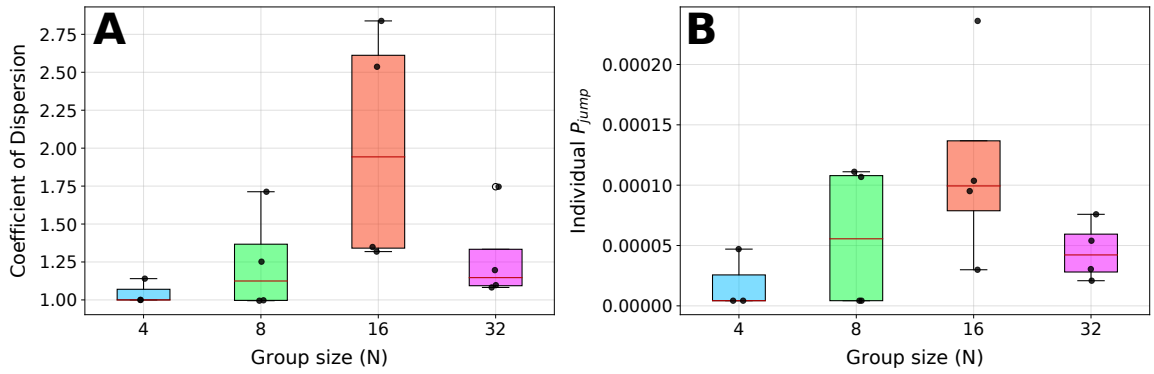

Figure 14. A Index of temporal dispersion over group sizes. CD was calculated using a rolling window with a size of 15 s. All values where normalized by corresponding group size. Raw data is shown as points. **B** Individual jump probability derived from the overall jump probability (see Equation 3.1), divided by the number of individuals in the corresponding group. Raw data is shown as points.

familiar sisters were less likely to jump into the unknown when compared to those paired with unfamiliar partners. Familiarity among these fish therefore reduced the overall jumping probability, and coinciding risk taking significantly. This is in contrast with our initial prediction that familiar partners should follow each other more readily into the unknown as compared to non-familiar individuals. As for larger group sizes an individual's probability to jump was found to be independent of group size, while showing an increasing trend with time spent in an unstructured and barren environment. The individual jump probability appears to be socially mediated given that nearly all groups showed a smaller than random difference in time between jumps and distance between jumps (see Figure 10). The only outlier in this case being the temporal difference in the group size N=4, where sparse data most likely doesn't allow for a conclusive statement.

Familiarity has been shown to have immediate fitness benefits in other contexts by leading to faster predator avoidance in brown trout *Salmo trutta* [82] and damsel fish (*Chromis viridis*) [161] and enhanced survival and body condition in Arctic char *Salvelinus alpinus* [198]. The here presented work is in line with these insights showing that familiarity decreases risk-taking and leads to enhanced survival. This holds to be true when taking into account the fact that the surrounding into which the fish displace themselves by jumping is unknown to them and could potentially lead to a higher risk when compared to remaining in proximity with a familiar individual under no proximate risk. Given the previous work staying close to a familiar partner leads to a better outcome and response when compared to an unfamiliar one, should a potential risk arise [82, 161].

Group size did not affect individual jumping probability, although group density was not specifically accounted for which also increased with group size, given the

fixed arena size. Further, to give more detail to the individual decision making process a leaky integrator and fire model (LIF) or drift defusion model would be a good extension to this work and is planned for future approaches. In the case of a LIF model The individual would receive input (e.g. visual stimulus or physical sound) about it's social partner's decisions. These would be integrated over time at an individual level with a certain proportion of 'leak' allowing the internal value to decay when no input is received. Integration is done until a certain threshold is met at which the individual makes a decision itself, resetting the internal value and leading to a behavioral change e.g. jump. A parameterized model as such allows for the individual level values (threshold, decay, attentiveness or accumulation value) to be estimated from the data to gain insights into the processes driving such individual and collective level behavior.

3.5. Conclusion

While gregarious animals have been shown to be affected by their social partners [127, 53] and may alter their opinion based on the behavior of others [183, 117] it is not always clear which behavior is socially mediated. The question to be answered in this work was whether jumping behavior of clonal fish was under social influence and how familiarity to social partners would alter this behavior. It was shown that the decision of jumping into a possibly unknown environment with unforeseen risks is socially modulated. In pairs familiarity facilitated longer waiting times and reduced likelihood to jump. In larger groups, both time and location of jumps were found to be socially dependent leading to subsequent jumps being in close spatial and temporal proximity of each other.
Familiarity has been shown to improve predator avoidance behavior in damselfish [161], while increasing inter-individual aggression in *P. formosa* used in this study [59]. It is likely that familiarity does not have a single effect on behavior and is in contrast highly context dependent. The Amazon molly shows effects of familiarity and is a good system to investigate familiarity and the co-occurring change of behavior over various time scales [138].

4. Behavioral Heterogeneity and Adaptation in Groups

Knowing that behaviors can be learnt and effected by conspecifics the question arose, to what extent individual behavioral differences play a role in this. Individuals learn at different rates and effect each other in their decisions, but are individual differences maintained in groups and are these constant or adaptive? These were the questions which motivated a subsequent piece of work to understand individual and group level behavior and their dynamics.

4.1. Introduction

Forming social aggregates is a common phenomenon among group living animals and has been shown to have many advantages for the individual, such as reduced predation pressure, higher foraging success and access to more sexual partners [127]. Among individuals persistent differences are apparent early in life [138] and arise due to varying factors such as experience [19], state [26, 156] and environmental stochasticity [92]. The ecological environment further shapes the way individuals interact with each other, and determines what kind of interactions are established in a social context [83, 88, 142]. Certain individual differences have been shown to diminish while others increase in a social context [90, 147]. Social groups of multiple, interacting individuals have further been shown to develop consistent traits of their own over time [241, 147]. By looking at individuals in a consistent social aggregation and habitat over time we can begin to understand the fine scale dynamics which change on an individual and inter-individual level. In the Amazon molly *Poecilia formosa* this has been done for individuals but not in a social context [138]. Therefore, this study set out to shed light on the dynamics behind such individual differences in persistent groups of interacting individuals. To do so the individual behavior was first recorded in a solitary setting and then consistently continued over four weeks in a group setting. An environmental variable was introduced to create novelty and variation among experience and to test how this would further effect differences among interacting individuals.

4.2. Methods

4.2.1. Animal Model and Husbandry

Here we used the naturally clonal fish species *Poecilia formosa* which was previously described (see Section 2) and was bred in the same animal housing facilities and reared under the same conditions (see Section 2.2.1). All animal experiments were conducted under the animal experiment number #0089/21 of the German State Office for Health and Social Affairs (LAGeSo). It was emphasised that all fish were unfamiliar with each other and the test environment at the beginning of the experimental phase, in order to reduce any effect of prior familiarization and habituation. For this study, roughly 100 female Amazon Molly (*P. formosa*) of similar age (1.5 months) and ranging from 20 to 30 mm in total length (TL) were manually sorted from stock population kept in a separated holding tank with gravel bottom and plants, a week in prior to the beginning of experiments. Fish were fed twice a day *ad libitum* with fish flakes and kept on a 12h:12h light:dark cycle, with water temperature around 24 °C and the water quality being measured weekly. In order to visually identify individual fish during manual sorting and automated tracking (Trex software trex.run), a total of 88 fish were marked with a color stripe on the left side of the body using Visible Implant Elastomer (VIE by Northwest Marine Technology, Inc.). Four highly distinguishable, fluorescent colours (red, blue, yellow and green) were used to mark the individuals, while the tagging equipment was prepared and used following the user's manual of Northwest Marine Technology. After a 3 min exposure of each fish to water with clove oil, a thin needle (standard insulin syringe) was used to implant the subcuticular tag in a way that it remained externally visible. Posterior to the incision, the needle was moved towards the fish snout, the material was injected as the needle was retracted leaving a color mark of 2-5 mm in length. All marked fish survived the procedure and none showed ill signs of discomfort, unusual swimming postures or aversive behavior. A week after tagging the total length (TL) was manually measured from the tip of the snout to the end of the caudal fin on a millimeter paper as well as photographed to get the standard length (SL) using the open source image processing program ImageJ 1.8.0 for later comparisons for each individual. After sizing, individuals were sorted into individual reusable plastic containers with water according to tag colours and were then randomly sorted into shoals of four individuals. In total 22 groups were formed with size matched individuals (± 0.2 mm), where each fish had a distinct and different tag color. These groups were then placed together in individual tanks of 10 L for acclimation without visual access to other groups, one week prior to the beginning of the experiments.

4.2.2. Individual recordings

Twenty-Four individual tanks (28 cm W × 28 cm L × 24.5 cm H) with water levels set to 4 cm were used to record fish individual behaviour. Tanks were individually labeled to provide identification in the videos. The arenas were illuminated from bellow using consumer grade LED lights in order to improve contrast and subsequent tracking quality. Before each trial a water change was performed after which the individual fish were randomized across all experimental tanks and allowed to acclimatise for 1 minute. Behavioral recordings were then done for 5 minutes each in an open field fashion, allowing the fish to move around freely. The sequence of recordings was randomized per day, in a way that a group would not be recorded twice a day and each individual would be recorded for three times over the course of all recordings. Recordings were done using two overhead cameras (Basler acA1920-155um, 1920 × 1200 px, grayscale, 30 fps) installed at a height of 80 cm and the Media Recorder software (Version 4.0.544.8 Noldus Information Technology, The Netherlands).

4.2.3. Group recordings

A round experimental tank (height: 50 cm, diameter: 74 mm⌀) made of opaque, white acrylic and was used to evaluate group behaviour over the course of four weeks. The circular tank was placed on a square pedestal surrounded by white curtains functioning as light diffusers. During experimental recordings the groups were exposed to two different environments inside the tank: 1) complex, with a total of eight white, small clay pots (height: 7 cm, diameter: 4 cm⌀) arranged in 2 concentric circles, four pots per circle (R1=25 cm, R2=12.5 cm) (see Figure 15); 2) simple, with nothing but water i n the tank. The water level of the tank was therefore set to 7 cm to ensure that all obstacles were covered but to be low enough to prevent the fish from passing over them. Water temperature was the same as in the rack system where the groups were kept (24 °C). Water was replaced at the beginning of every recording day and fish were always tested prior to having been fed. The sequence of recordings was chosen randomly taking into account that a single group should not be exposed to both environments on the same day, hence three days were needed to complete one training session with all the groups and this procedure was repeated for four weeks. Recordings were done for 10 minutes with 1 minute acclimation time. Video observations were acquired using an overhead camera (Basler acA5472-17uc, 3400 × 3400 px, RGB, 15 fps) installed at a height of 130 cm and using the Motif video recording software (loopbio GmbH, Vienna, Austria).

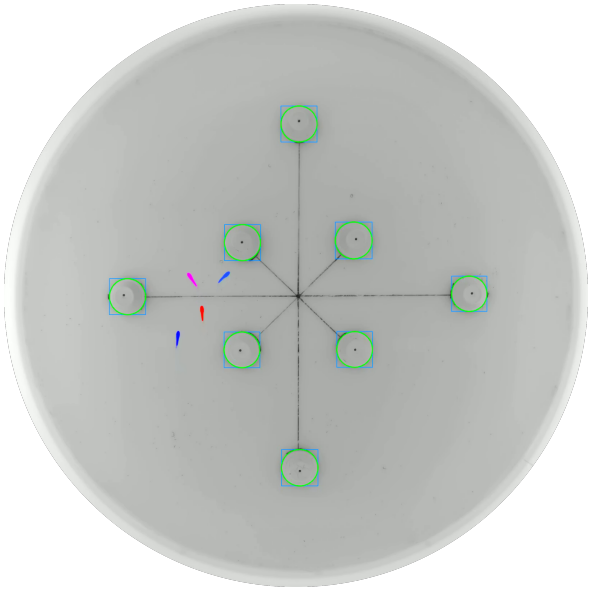

Figure 15. Top-down view of the experimental tank used for group behavior recordings showing a complex environment setup and four individual fish. Obstacles (green/blue) and fish were automatically detected and tracked over time to get exact locations in each frame

4.2.4. Analysis

From the individual and group recordings trajectories were retrieved using openly available tracking software which is capable of maintaining individual identities and capturing their posture over the course of the recordings [230]. These individual trajectories were manually corrected and matched across all recording instances to achieve continuous tracks for all individuals and across all recordings. This allowed us to analyse the correlation between individual median swimming speed alone and that shown when swimming in a group as well as individual variance and inter-individual variance over time. Individual trajectories were interpolated after which the median speeds were calculated, resulting in individual time series for recording. Swimming speeds were then filtered to be between 0 and 20 cm/s in order to remove extreme outliers which were mostly due to interpolation of erroneous tracking instances.

Statistical Analysis

All statistical analysis was done in R (v4.2.2 'Innocent and Trusting', `lme4` v1.1-29) and Python (v3.8.0, `scipy` v1.10.0). Statistical models were designed according to the experimental setup and finding the best appropriate architecture via conditional

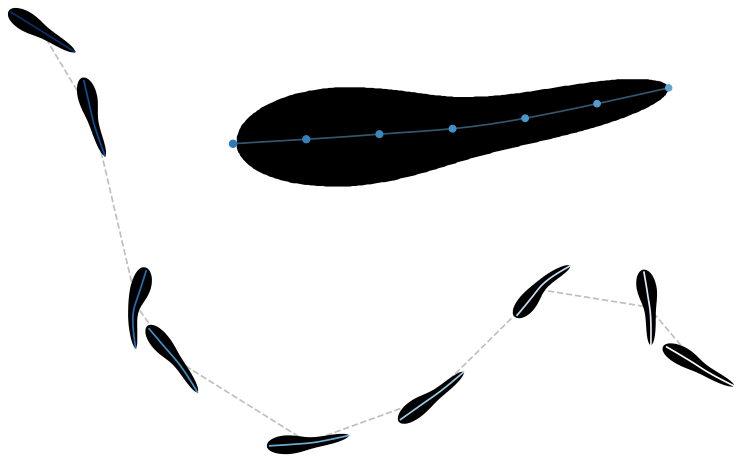

Figure 16. Example trajectory of a single fish over the course of 3 seconds sampled at 5 Hz. Superimposed is a contour, highlighting the midline and the 7 points distributed along it which represent the fish's posture and detail of tracking.

Akaike information criterion (cAIC) (`AICcmodavg` v2.3-1). Consistent inter-individual differences were established following the variance decomposition according to Nakagawa and Schielzeth [163] and using the openly available software package (`rptR` v0.9.22, nboot=1000, npermut=1000, [210]).

4.3. Results

Behavior in Solitude

A total of 88 individuals, corresponding to 22 complete groups were analyzed in respect to their individual behavior recorded alone, without social context. A Gaussian linear mixed-effects model was used to analyse the effect of repeated measures and initial size on the individual swimming speed. To account for consistent inter-individual differences across three consecutive measurements, individual ID was incorporated into the model as random effect. Overall the model's total explanatory power was weak (conditional R^2 = 0.06) and that related to the fixed effects alone (marginal R^2) was of 3.43e-03 (see Supplemental Material Table 5). The model's intercept, corresponding to the average median speed observed across all individuals in the first recording (date_index = 0), was found to be at 0.52 (CI=[0.36, 0.68], t_{255}=6.36, p<0.001 ***). Both initial size and time, as subsequent recording index in days, had no significant effect on the performed median swimming speed (β_{date}=-0.03, CI=[-0.08, 0.03], t_{255}=-0.90, p=0.369; β_{size}=-6.88e-03, CI=[-0.05, 0.03], t_{255}=-0.34,

p=0.734). Over the course of the measurements in absence of social partners, the individual behavioral consistency, given as repeatability or within-individual variance was weak and non-significant (R=0.06, CI=[0, 0.185], p=0.197).

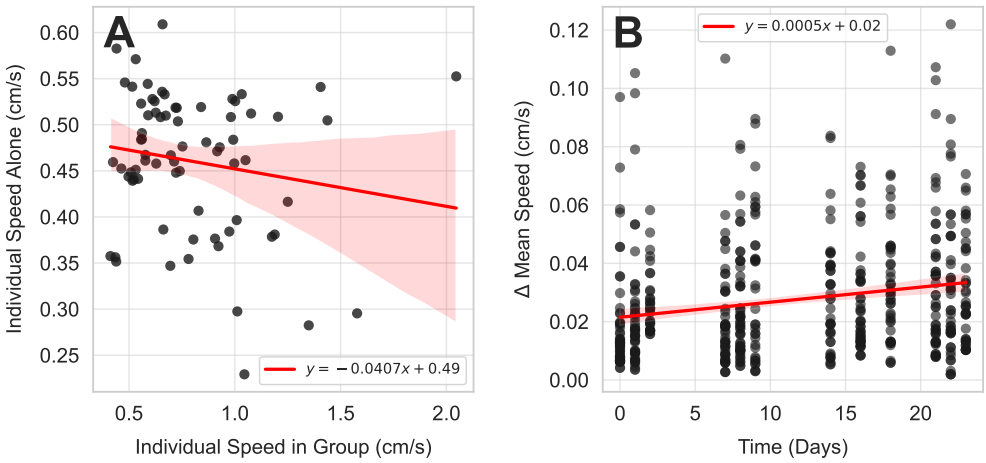

Figure 17. A Individual average swimming speed is plotted against the individual swimming speed within a group. Each point (black) represents one individual. **B** Difference between mean individual speed and that of the group partners for all individuals (black) over the course of the experiment. Linear trends are shown as first degree least squares polynomial fit (red)

Behavior in Social Context

A total of 72 individuals, corresponding to 18 complete groups were analyzed in respect to their individual behavior with and without social context. Individual swimming speeds recorded in social isolation were not significantly correlated to those retrieved in the social context (Spearman: r_{72}=-0.102, p=0.393, n-permutations: 10000; retrieved with subsequent permutation test, for correction of low sample size, Figure 17A). However, the difference between the individual speed and that of the other group members was found to be positively correlated with subsequent recordings (Spearman: r_{536}=0.240, p<0.001 ***, n-permutations: 10000; retrieved with subsequent permutation test, for correction of low sample size, Figure 17B).
Only individuals for which the first and last recording instance were included in the analysis were considered for this comparison. Overall the individual speed decreased over the course of time (see Figure 18). This decrease across individual speeds between the initial and the last experimental trial was significant in the case of the complex environment (Paired T-Test: t_{11}=5.48, p<0.001 ***, Figure 18) but not significant in the simple environment (Paired T-Test: t_7=1.69, p=0.135, Figure 18).
A Gaussian linear mixed model was used to predict the detailed effect of individ-

ually recorded speed, body size (TL, cm), environmental complexity and subsequent test days on the median group speed in each recording instance (formula: group_median_speed.cm.s ~ ind_speed.BL.s + size.cm + environment + date_index). To account for consistent inter-individual differences, individual ID was incorporated into the model as random effect. The model's total explanatory power was substantial (conditional R^2 = 0.56) and the part related to the fixed effects alone (marginal R^2) reached 0.25 (see Supplemental Material Table 7). The model's intercept, corresponding to the average median group speed for any given individual when first being introduced to the group arena (date_index = 0), was estimated at 0.42 (CI=[0.10, 0.73], t_{829}=2.60, p=0.010). Reduced environmental complexity (simple) had a significant, positive effect on the group swimming speed, although overall the swimming speed significantly declined over time (β_{env}=0.08, CI=[0.07, 0.09], t_{529}=11.20, p<0.001; β_{time}=-5.62e-03, CI=[-6.49e-03, -4.75e-03], t_{529}=-12.69, p<0.001, see Figure 18). Individual speed recorded in isolation showed a negative effect, while individual body size had a positive effect on group speed (β_{speed}=-0.10, CI=[-0.38, 0.18], t_{529}=-0.70, p=0.484; β_{size}=0.04, CI=[-0.09, 0.16], t(529)=0.56, p=0.574). However, both individual speed in isolation, as well as initial body size were not found to be of statistical significance.

Similarly, the effect of subsequent recordings, initial speed, body size and environment on the individually expressed median swimming speed within the group produced similar results. The total explanatory power of the model was substantial (R^2 = 0.56, conditional R^2 = 0.24) with an intercept at 0.49, corresponding to the average individual speed across all groups at the beginning of the experiment (CI=[0.17, 0.81], t_{529}=2.98, p=0.003) (see Supplemental Material Table 6). Time, as subsequent days negatively influence the individual swimming speed, reducing it significantly, while reduced environmental complexity significantly increased the individual swimming speed (β_{time}=-5.69e-03, CI=[-6.58e-03, -4.79e-03], t_{529}=-12.51, p<0.001; β_{env}=0.08, CI=[0.06, 0.09], t_{529}=10.82, p<0.001).

To estimate the within-individual variance components the same model was used as previously described. Individuals showed significant consistency in their median individual swimming speed across all repeated measurements of being observed within their groups (R=0.421, CI=[0.31, 0.523], p<0.001 ***). To further test for the effect of environmental complexity on the individual behavioral variation in median swimming speed the repeatability analysis was performed on the data subsets for each environmental treatment ('Complex', 'Simple'). While the individual behavioral consistency was significant in both cases, it was slightly elevated in the simple and non-occluded environment ($R_{complex}$=0.426, CI=[0.283, 0.552], p<0.001 ***; R_{simple}=0.449, CI=[0.307, 0.565], p<0.001 ***).

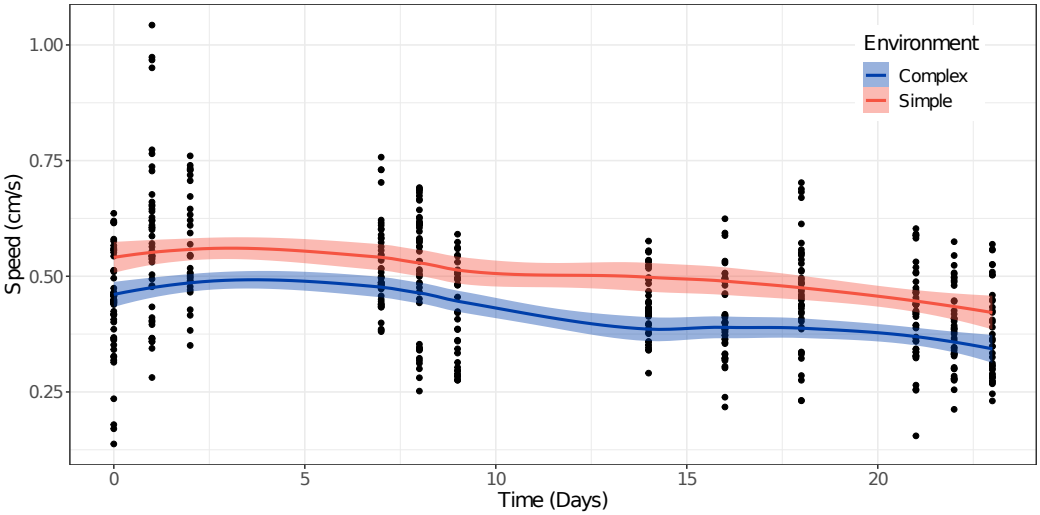

Figure 18. Visualization of the individual speed separated by environmental treatment and shown over the entire experimental period of four weeks. Each point represents an individual median value for a 10 min. recording interval. Smooth fit represent linear mixed model estimation with corresponding confidence interval

4.4. Discussion

Considering individual behavior under the influence of the social environment and in isolation helps understand the interplay between individuals and their social context. In this work we show that individuals exhibit different behavioral traits i.e. median swimming speed depending on the availability of social partners (see Figure 17A). The overall speeds were lower compared to those shown in similar studies [138]. When alone, we observed low individual consistency in the swimming speed, which increased in the social context. The effect of social partners has been shown to influence behavior in humans [241, 17] and other non-human species alike [90]. This is in line with our findings that individual behavior observed in solitude does not fully predict the behavior expressed in a social context. However, Herbert-Read et al. [90] found that individuals adjusted their speed to each other leading to higher social conformity in groups and less individual variability of swimming speeds. In the here presented data, we were able to reproduce the finding that individuals reduce behavioural variability i.e. showing higher repeatability and individual consistency in social groups (see Section 4.3). However, in this work individuals showed highest social conformity on the first day of recording, where habituation and familiarity can be expected to be lowest. This conformity decreased over time, leading to the highest differences among median swimming speeds of the individuals within a group on the last day of recording (see Figure 17B)).
The complexity of the physical environment has been shown to alter the observable behavioral variability in fruit flies *Drosophila melanogaster* [5] and rats *Rattus*

norvegicus [240]. In the here presented work, individual Amazon mollys likewise showed elevated behavioural variation in a simple non-occluded environment, when compared to an environment of higher structural complexity (see Section 4.3).
Besides physical complexity, temporal aspects were found to greatly influence the individual swimming speed within groups. This would be expected due to habituation, a form of adaptation to both the physical and social surroundings taking place over time and subsequent exposures [216]. Responsiveness and the transfer of information have been shown to be dependent on swimming speed in fish schools, which can in turn allow the individuals to adapt their speed to the informational requirements of the situation [169]. In an uncertain environment, as is the case in the initial recording prior to any experience speed would be kept low to be more responsive to the neighbors and other external stimuli. Over time certainty is established and habituation takes place allowing for higher individual swimming speeds within the group. Although in the here presented work individuals show increasing individual differences in swimming speeds over time (see Figure 17B), the speed was not found to be lowest at day 0. However, it is lower in the convoluted environment which can be seen as suggestive evidence of the uncertainty argument (see Figure 18). The process of habituation most likely is not linear, where more rigorous testing would be advantageous to highlight the causal effects. Methodologically however this already emphasizes the importance of acquiring multiple repeated recordings in order to establish a representative value, even for such reduced behavioral traits as swimming speed might be seen as.

4.5. Conclusion

Aggregating towards likewise behaving individuals has many benefits for gregarious animals, such as the diluted risk of predation and higher foraging success [127]. However, a question that remains unanswered and for which we still lack sufficient experimental studies, is what fitness cost is associated with being individually flexible compared to being more stubborn in such social scenarios. Given that individuals often show high levels of inter-individual variation and, as shown in this work, are capable of adaptively changing it according to the physical and social environment, we may pose the question as to when this change is advantages and when not. In times of sparse information or high uncertainty this can lead individuals to be more responsive to their environment, in turn leading to higher conformity. This need not be an active decision at the individual level and could merely be a mechanism to deal with limited attention [63] but inherently allows for more efficient flow of information and subsequent distribution of knowledge [169]. Building on the ability to record individual behavior over long periods of time and in high detail (see Laskowski et al. [138]), while keeping track of the individual identities even in a

social context the ultimate and proximate causes of individuality and it's adaptations should further be explored. Possibly the most intriguing aspects of such studies are the temporal dynamics of behavioral change taking place over various timescales. Within seconds the location can be changed leading to new sensory input while over days, weeks and years adaptation can take place and information can become learned and ingrained into consistent behavioral traits. These aspects of behavioral research are often complicated to capture and distil but hold much potential for future work.

5. The Effect of Motile Prey on Swimming Activity

To recapitulate, by now we know individuals learn, show consistent individual differences and are effected by conspecifics in their behavior. But how does the physical surrounding and the experienced variability of such effect the behavior? As alluded to in the previous work on individual and group level processes, the physical environment has a significant effect on the behavior being observed and cannot be excluded in such studies. This is mainly due to the fact that the environment can shape experience and, in turn behavior [5]. The following work was motivated by the question whether food availability in the environment would have an effect on certain behavioral traits, such as swimming speed.

5.1. Introduction

On the one hand animal behavior has become increasingly interesting for aquaculture facilities as means of managing livestock health and animal welfare [49, 10]. On the other hand, the research field of animal behavior has been interested in observing and understanding natural behavior for decades [157, 219]. Live prey has regularly been used to foster fish growth and larval survival in marine and freshwater husbandry facilities across the world [18]. The Japanese water flea *Moina macrocopa*, a commonly used live feed in commercial aquaculture, is frequently used along side brine shrimp *Artemia* for larval rearing in many ornamental and agricultural fish species [108, 181]. Yet little attention is drawn towards the effect of using naturalistic, live food on the behavior in behavioral ecology [101, 107], while this is a well studied field in aquaculture. Environmental complexity, as experienced by an individual, has been shown to effect the behavior in fruit flies *Drosophila melanogaster* [5] and rats *Rattus norvegicus* [240], and has been touched upon in the sections above (see Chapter 4). Further, animals conditioned on unreliable food sources have been shown to increase their foraging effort in order to compensate for potential food shortage - A process termed "incentive hope" by Anselme and Güntürkün [8], which can shape the foraging behavior [7].
The Amazon molly (*P. formosa*), is a naturally occurring clonal freshwater fish. This all-female species originated from a rare hybridisation event between a male Sailfin molly (*P. latipinna*, ♂) and a female Atlantic molly (*P. mexicana*, ♀) dated back to about 100.000 years ago [94, 194, 197, 136, 209, 231]. These highly social fish are of interest for the understanding of consistent inter-individual differences and the development of individual heterogeneity in light of environment and experience [26, 140, 141].

Here we set out to test the effect of live prey on the open field behavior. In particular we were interested in testing whether changes in swimming speeds, as proxy for foraging effort would take place in response to food availability. First, we established a feeding regime for three treatment groups. These consisted of commercial dry food, fresh non-motile prey and live motile prey. Subsequently, we tested for differences due to the treatment, in growth rate and behavioural traits such as preferred speed.

5.2. Methods

Experimental fish were kept individually in 12 L tanks (14 cm W × 40 cm L × 20 cm H). These individual tanks were part of a circulating water system with a common sump reserve and filter (total volume: 400 L), while the outlets where blocked by fine sponge material. This was done to maintain stable temperature and continuous water exchange, while keeping food particles constrained inside the individual tanks. The rack system was further supplied with a UV sterilized (deBary 25 W) in order to reduce the overall bacterial load. Fish were kept on a rigorous feeding regime of commercial dry food ('Comercial'), freshly killed *M. macrocopa* ('Dead') or live *M. macrocopa* ('Live') over the course of four weeks, with food being distributed once a day. Commercially fed individuals received 0.001 g flake food (TetraMin Flakes), while all other treatment groups received *M. macrocopa* which were strained through a 100 µm mesh, to ensure same maximal size and rinsed with fresh water. Live fed fish were then fed with *M. macrocopa*, while dead fed fish were fed with freshly killed (frozen) *M. macrocopa*. Each individual fish was given 3 mL of the well mixed *M. macrocopa* solution, of which the prey density was automatically determined, using a custom script based on object detection (see 'Thing_counter.py', see Figure 19) and recorded for each feeding instance and individual. To record growth we used a custom developed, freely available, open-source measuring software for semi-automatic measuring based on images, ensuring controlled and reproducible results [2]. Size of the fish, measured as Total length (TL), was recorded once per week using the freely available measuring software. This allows us to establish a growth curve across all individuals and treatment groups.

5.2.1. Video and Image Analysis

Over the course of four weeks, all individuals were checked for size differences and subjected to one behavioral, open field recording every week in absence of food. Individual recordings were done once a week for 60 minutes and using overhead cameras (Basler acA5472-17um, 3684 × 3684 px, grayscale, 15 fps). Sizes were measured as total length (TL) and recorded using semi-automatic procedure to reduce experimentor bias. However, to ensure comparability and test the accuracy

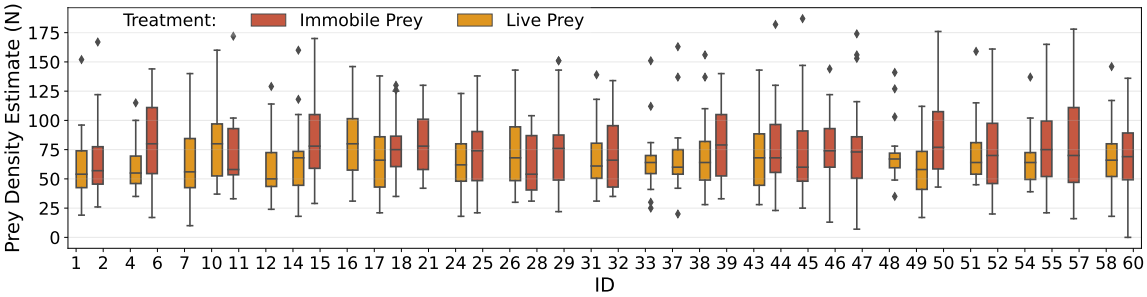

Figure 19. Administered prey densities received by each individual in the corresponding treatment groups

of the automated methodology, all individual were also manually measured from top-down images (Fiji v2.9.0) (The comparative work is not included in this thesis). From the automated measurements the individual growth curves were established.

5.2.2. Postprocessing and Statical Analysis

Post-processing of the obtained trajectories and data was done in Python and subsequent statistical analysis using R (v4.2.2 'Innocent and Trusting'). Median speed was calculated by tracking the individual fish using openly available software [230] and subsequently calculating the metrics for each session from the time series of cartesian coordinates (x,y). From the trajectories the instantaneous speed was calculated as time series for each individual and recording and filtered to be within the range of 0 - 20 cm/s. Outliers were further removed from the median speed calculation by the standard deviation of these time series. Data points with a standard deviation of speed outside the range of two standard deviations from the mean of all data points were excluded (Mean $\pm 2 \times SD$). This was done to account for tracking inconsistencies leading to increased speed.
For the analysis using a Linear mixed-effects model approach, models were constructed with gaussian error distribution using the library `lme4` (v1.1-29) and best fit was established through comparison of the corrected Akaike information criterion (cAIC) (aictab, `AICcmodavg` v2.3-1) and automatic model design (`buildmer` v2.8). The model with the lowest cAIC as well as all models within 4 ΔcAIC units are considered equally supported. Initial size and test tank were included as fixed effects to account for any initial variance among individuals in size and their randomly assigned recording arenas. Where appropriate and to further account for individual variation a random effect in form of a random intercept was added for each unique ID (`rptR`, v0.9.22).

5.3. Results

At the beginning of the trials a total of N=20 individual fish were included in each treatment group, resulting in a total of N=60 fish. Three fish were removed prior to reaching the end of the experiment at day 40 due to poor health which resulted in a total of N=57 successfully reaching the last day of trials. However, for consistency the measurements of all individuals were incorporated into the final analysis. Growth was established as the size increase over the course of the experiment and growth rate as the increase in size per time unit (day).

5.3.1. Growth

Growth rates were obtained across the entire experimental duration of four weeks and across all treatment groups (see Figure 20). A Kruskal-Wallis test was performed to test for the effect of feeding regime on growth rate, which revealed a significant difference between treatments (H_2=28, p<0.001 ***). Conventionally fed fish showed the highest total growth ($\langle x \rangle_{\text{conv}}$=2.65 cm, $\langle x \rangle_{\text{live}}$=2.09 cm, $\langle x \rangle_{\text{dead}}$=2.12 cm; Dunn post-hoc test with Benjamini-Hochberg p-value adjustment: Conventional - Dead, p<0.001 ***; Conventional - Live:, p<0.001 ***; Dead - Live: , p=0.694).

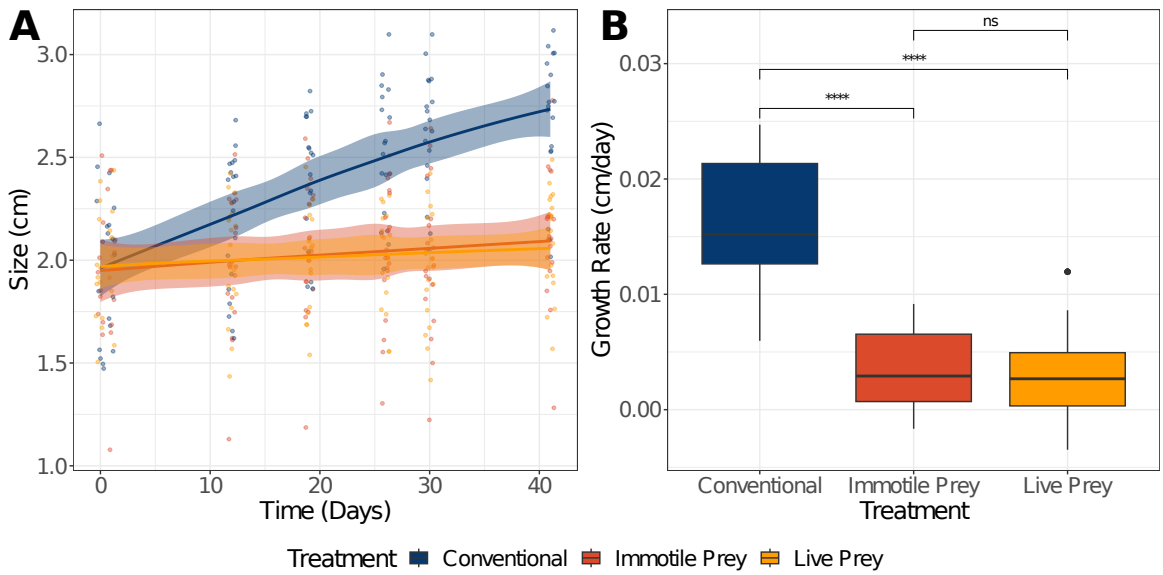

Figure 20. A Individual size over the course of the experiment and across all individuals (N=20) per treatment group. Raw data is shown as points with jitter added for better visibility. A model fit is shown as line with 95% confidence intervals given as shaded area. **B** Growth rate across treatment groups. Asterisks indicate results from post hoc pairwise comparisons

5.3.2. Speed

Concerning the behavioral response in swimming speed there was no observable difference between the median swimming speeds across treatment groups. The effect of food treatment on the median speed was analyzed using a linear mixed model with time, treatment and the initial size added as fixed effects. The suggested model of best fit did not include treatment or a random effect which were added for experimental representation and consistency. The final model was fit to the behavioral response across all individuals (N=58). A random intercept was added per unique individual to account for individual variance across repeated measurements (formula: MedianSpeed ~ InitialSize + RecordingIndex + Treatmemt + (1 | ID)). The total explanatory power achieved by the final model was substantial (conditional R^2 = 0.31, marginal R^2 = 0.27) (see Supplemental Material Table 8). Concerning the estimate of the fixed effects, the initial size had a significant, positive effect on the median swimming speed, while time had a significant negative one (β_{size}=0.51, CI=[0.29, 0.73], t_{199}=4.58, p<0.001; β_{time}=-0.03, CI=[-0.04, -0.02], t_{199}=-7.71, p<0.001). In other words, initially larger individuals swam faster, while over time all individuals reduced their swimming speed. There was no significant effect of treatment on the median swimming speed (F_2=0.0.453, p=0.638; see Figure 21). Variability among individuals measured as variance component accounted for by the random effect was low and non-significant over repeated measurements (R=0.056, CI=[0, 0.206], p=0.286).

To test for the effect of prey density on the median speed and to account for variability in food availability among days a similar approach was taken. However, for this comparison only the two treatment groups fed on a *M. macrocopa* diet were used. This was done, given that the other treatment group, fed with conventional food did not experience any daily variability in food availability. The same statistical model as previously described was used with the addition of daily, individually received prey count as fixed effect (formula: MedianSpeed ~ InitialSize.mm + Treatment + RecordingIndex + PreyCount + (1 | ID)). Again, the explanatory power achieved by the final model was substantial (conditional R^2=0.37, marginal R^2=0.32) (see Supplemental Material Table 9). The prey count was not found to have any significant effect on the swimming speed (β=-5.05e-04, CI=[-3.57e-03, 2.56e-03], t_{127}=-0.33, p=0.745) while initial size and time remained to have a significant positive and negative effect respectively on the swimming speed (β_{size}=0.68, CI=[0.37, 0.99], t_{127}=4.32, p<0.001; β_{time}=-0.03, CI=[-0.04, -0.02], t_{127}=-6.65, p<0.001). Daily variation in prey abundance therefore did not significantly affect the observed swimming speeds.

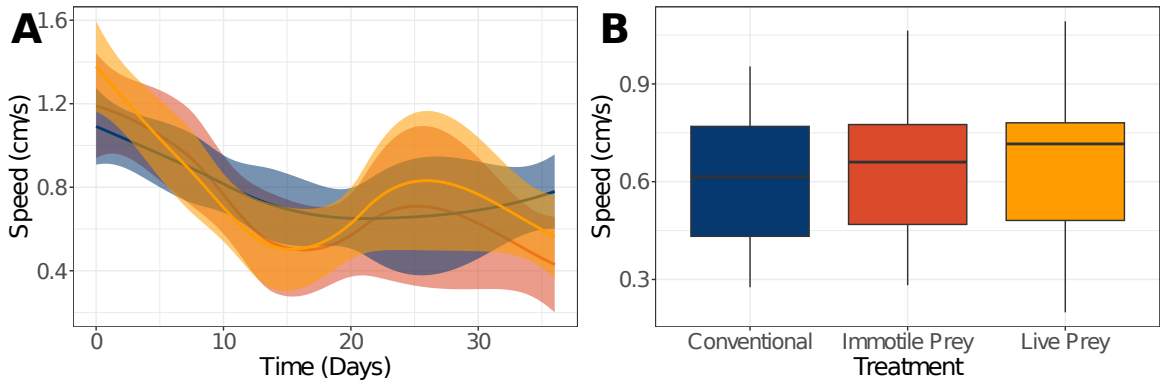

Figure 21. **A** Median swimming speed over time and show across treatment groups; **B** Overall median swimming speed across treatments

5.4. Discussion

In this study we set out to determine the effect of food regime and prey motility on the swimming behavior of fish. We see significant difference in growth across treatment groups, where the group fed with commercial food showed highest increase in total length (see Figure 20A). Although live and naturalistic prey can lead to enhanced feeding behavior [181] it can also introduce pathogens such as *Vibrio spp.* to the system [18]. The fish in this study were examined daily for infections and other anomalies. Over the course of the experiment three fish (one of each treatment) were removed due to such irregularities, suggesting that the difference between the treatments is likely not due to any infection. It is more likely that the effects are due to nutritional differences between live prey and conventional food, especially given that prey fed diets (live and immotile) showed the same growth rates (see Figure 20B). Contrary to the initial assumption there was no treatment level effect of diet on the median swimming speed (see Figure 21). This can be due adaptations such as the adjustment of foraging activity to the nutritional demand, by which individuals receiving a low nutrition diet would compensate by increase foraging effort [135]. An increase in foraging effort would be reflected in a higher median speed, which is suggestive in the early trials of the live and immotile prey treatments. However, given that the fish were always fed after the behavioral recordings this is likely by chance and not due to any treatment effects. Prey fluctuations were not found to have any significant explanatory power for predicting the median swimming speed (see Section 5.3.2 and Figure 21A). This further suggests that no behavioral adaptation in response to food availability took place in these animals. The fact that the animals are capable of learning when and where food was presented could further explain the lack of treatment level differences in behavior [41]. Animals would then adjust their foraging strategy to match the timing of food availability more closely.

5.5. Conclusion

This study set out to test the influence of live prey and motile prey on the swimming behavior of captive, naturally clonal fish. In the here presented work diet composition and food motility had no effect on the recorded behavior and did not lead to any strategy shift towards increased exploration [150]. Adding live prey to the diet of captive, lab reared animals can enhance survival and lead to more naturalistic behavior [135]. However, the here presented results show no alteration of behavior in form of swimming speed allowing for comparable results across diets. Although, adaptation of exploration behavior to nutritional needs can take place it was not apparent in this experiment suggesting that fluctuations in prey densities did not lead to immediate nutrient deficiencies [135]. Importantly, this work allows for insights and applications of more naturalistic circumstances and conditions in lab based behavioral studies. In order to study naturalistic behavior such attempts need to be made to recreate more natural conditions under which behavior can be observed even under laboratory conditions [157, 118].

6. Quantitative Tools for Ethological Studies

6.1. Unsupervised Behavioral Quantification

Given that behavior takes place across multiple time scales (e.g. shaking a hand vs. learning to walk) behaviors are not always easy to quantify [33, 4]. Observing animals and noting their actions according to standardized reference catalogues i.e. ethograms has been the standard approach in behavioral research. With the advent of computer assisted methods to analyse complex data, behavioral quantification can now be done using unsupervised and programmatic tools [22, 33, 4]. To find behavioral differences, bridge these approaches with established methodologies and test their utility, both manual and automated methods were tested on an empirical behavioral data set as shown in the following.

6.1.1. Introduction

Behavior, as the context dependent response of an individual to it's environment, commonly exhibits high levels of variation in natural systems [165]. This variation can stem from a multitude of sources, such as inter-individual differences in morphology, genotype or experience [92, 81] allowing for the distinction between intra- and inter-individual variation. Intra-individual variation refers to the difference within a certain behaviour, which an individual may express and inter-individual variation accounts for the variation among individuals. Such variation at the individual level can further be broken down into variation among and within behavioural elements i.e., elementary motor acts and postures following the description of [221]. These elementary units of behavior can be combined and reorganized to form a multitude of motor patterns or behaviors, analogous to proteins being composed of various amino acids. Consistent individual traits have become an aspect of interest among many fields, with specific focus drawn towards ethology, ecology and evolution. The variation among individuals has been well documented and continues to give promising results [26, 140, 139]. However, the role of such individual differences within a group or collective is still underrepresented in this body of work. Although of great interest, little research has focused on the conditions under which individual differences are expressed or when these are diminished and the dynamics controlling such processes. The field of collective behavior has produced ground breaking insights into the functionality of collectives and answering the question of how multiple agents may interact to create a collective behavioural state [53, 226] or highly coordinated predator response [60]. Yet an aspect which many of theses studies have in common is the often made assumption, that all individuals are following

the same behavioural rules and acting upon the same information [228, 53]. Given the substantial evidence of individual differences there has been a growing interest in the interaction between individual heterogeneity and homogeneous collective behavior, eluding towards the importance of considering both [103, 104]. This combined with the fact that it is now becoming possible to determine individual behavioural differences at an unprecedented spatio-temporal resolution [138] and under complex natural conditions [212, 66, 123] we are now able to apply quantitative methods for behavioral classification to such data in an unsupervised manner [33]. Such behavioural quantification methods which enable the classification and quantification of minute behavioural changes at the sub-second level are capable of determining inter-, and intra-individual variation. They further allow fine scale analysis of variation at the level of the behavioural elements, enabling the comparison of specific motion patterns and study of developmental changes along behavioral axis [208, 22, 122, 33, 92, 81, 229, 118]. More generally, these methods enable objective analysis, standardized interpretation and reduce confirmation bias in behavioral studies [151].
Here, we set out to compare manual observations used as reference data to one such unsupervised behavioural quantification method. Highly stereotypic behaviour of the live bearing, freshwater fish *Poecilia mexicana* which is endemic to central America was analyzed [159]. Specifically, male *P. mexicana* fight for access to sexual partners and to establish dominance which has been shown to follow ritualized and highly stereotypic rules [25]. Behaviors and traits shown in such fights are often under natural selection, as they serve as an honest signal of health and strength to any bystander or potential mate [38]. Given the importance of such behaviors and the information they contain, the goal of this study was to determine small scale variation in behaviors among two fighting male *P. mexicana* and test whether a behavioral signature exists which allows the prediction of the fight outcome. Thus, in addition to comparing the performance of the two, manual and automated behavioral labeling methods, the outcome of adversarial interactions was quantified on a fine scale using behavioral time series in 3D.

6.1.2. Methods

Tracking and Data Collection

Individual, male *P. mexicana* were combined with conspecific males into size matched pairs. Males of this species commonly initiate fights to establish dominance and these fights are composed of highly stereotypic behaviours and usually end with a clear winner and loser. Each individual was subject two two recordings, where the partners were re-shuffled between recordings. Pairs were introduced to a calibrated imaging tank equipped with a circulating water system. Fights were recorded from

three angles synchronously using a custom recording interface (Loopbio, Vienna; Basler acA2040-90um, 2048×2048 px, grayscale, 50 fps). A recording consisted of six minutes acclimation time, after which the fish were allowed to interact. The a recording ended when no aggressive interactions were observed for ten consecutive minutes or a clear outcome, signified by winner and looser was achieved. The outcome was determined by one individual showing clear appeasement behavior towards the other and/or fleeing. Each camera head was calibrated using a custom script and utilizing the computer vision library OpenCV [102]. Individual tracking was done in 2D for each view independently, using a mask based, deep neural network [1] to consistently detect the fish from all angles. Network initiation and training was done following the procedure described in [66]. Individual tracks were checked for false detections and other inconsistencies and manually merged using the openly available software tool TrackUtils (see supplemental materials Francisco et al. [66]), which was custom designed for this task.

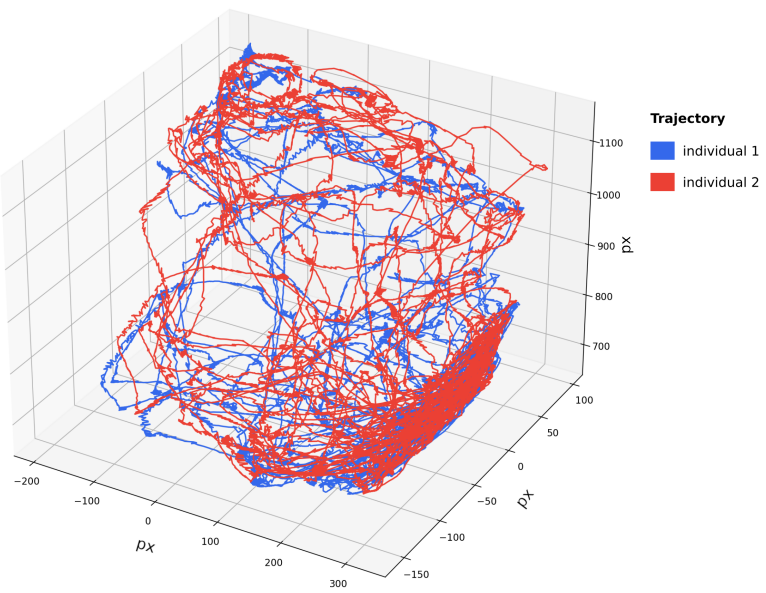

Figure 22. Example reconstruction of the 3D trajectory of two interacting fish

Detections were tracked for each individual in 2D for each synchronized camera head (viewing angle) independently, resulting in time series of length of the video for each coordinate (x, y). Three dimensional trajectories were acquired in a consecutive step through pairwise triangulation of 2D detections from two views, using a custom pipeline. Output in this case was a three dimensional trajectory which served as raw input to the unsupervised behavioural quantification pipeline.

Manual Annotations and Ground Truth Dataset

All fights were manually viewed and the time points classified with the corresponding behaviours using the software BORIS [68]. Behavioural categories were drawn from a classical ethogram, following Bierbach et al. [27] and Bierbach et al. [25]. This resulted in the ground truth data set to which all further unsupervised findings were compared to.

Behavioural Quantification

For each individual, trajectories along the three spatial axis (x, y, z) and with length of the video, are used to further calculate instantaneous speed and direction along the x-y plane. The speed and direction along the x-y plane was chosen, as fish tend to move more along these axes and not as much along the z dimension. To reduce computational load data was extracted at 25 Hz and was processed in the further steps. By applying a wavelet transformation with 100 frequency bands to the signal time series each point in time (frame) is represented by 100 dimensions, while adding a time dependent component (see signal.cwt in scipy v1.10.0). From the transformed signals only every other of the hundred frequencies was used for further analysis, resulting in a 50 dimensional feature vector for each time point i and each of the input metrics (x, y, z, speed, direction). Every other frequency band is chosen to span a wider range of temporal scales, as opposed to using 50 signal frequencies directly during the wavelet transformation. The resulting total feature vector v amounts to $v_i \in \mathbb{R}^D$ where $D = 5 \times 50 = 250$ for each time point i along the time series ts for a given individual $n \in 1, ..., N$, where $N = 16$ is the total number of individuals. This dimensional fan-out step serves to increase the feature space describing a single observation and adds a temporal component to an otherwise discrete measurement. In order to predict behavioural classes a hourglass neural network, also know as autoencoder (see Figure 23) is trained on a all data, in shape of a single data frame. The data frame was constructed as a concatenation of all individual time series wavelet transformations. For every individual $n \in 1, ..., N$, each times series ts_n, with the dimensions $250 \times t_n$ was stacked on to the next time series block along the first dimension resulting in a 134016×250 data frame. This serves as input to the encoder and allows it to be trained iteratively ,where the weights of the model are updated row by row. The aim here is for the encoder to learn lower dimensional representations within the data [153], which has been shown to be useful when applied to behavioral data [15, 154, 110, 51, 4, 164]. Further, by doing so the similarity between time points is evaluated based on the wavelet transformation, which takes the temporal neighborhood of a certain time point into account.
Using the autoencoder approach allows for continuous updating and streaming

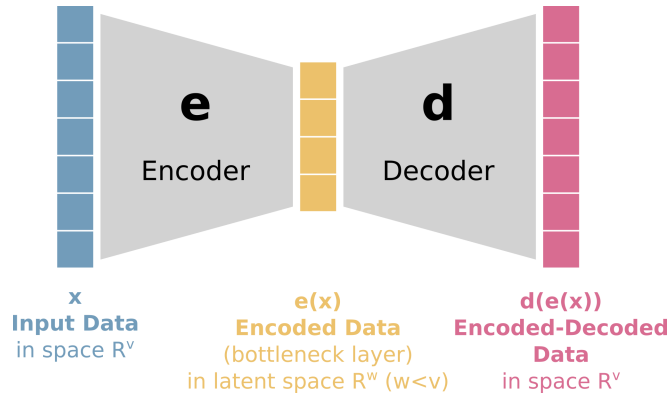

Figure 23. Schematic of a standard autoencoder architecture containing input, encoder, decoder and output

of new data, while avoiding computational bottlenecks. An added benefit of such approaches is that once trained, the network/model can be applied to predict the behavioural states. This is done by supplying the trained encoder with a new input vector of same shape as the previous training data, from which it will generate a lower dimensional representation or encoding. This representation is then drawn from the bottleneck (smallest and most central; here 15 Nodes) layer, where information is condensed most. Each node of the bottleneck layer accumulates distinct information about the input data and is therefore forms a abstract representation of it. These are similar but not the same as the principal component axis or eigenvectors in other approaches to reduce dimensionality. For large bottleneck layers an additional step can be added to reduce the dimensions further. This is achieved by applying Uniform Manifold Approximation and Projection (UMAP) to the bottleneck layer output (see https://umap-learn.readthedocs.io/en/latest/). By using UMAP the dimensionality of the autoencoder output is reduced to two dimensions. In the here presented approach the autoencoder output, taken from the bottleneck layer (15 dimensions), was directly clustered using a hierarchical extension of the Density-Based Spatial Clustering of Applications with Noise algorithm (DBSCAN), termed HDBSCAN (see https://hdbscan.readthedocs.io/en/latest/index.html) [46]. This is a highly efficient yet conservative approach which results in labels for each time point, while excluding noise or uncategorized data. Each point within the final, two dimensional point cloud represents an individual time point, where these time points are clustered based on the high-dimensional similarity along their initial feature vector (v_i). The number of clusters and cluster association is mainly determined by the minimum cluster size, which defines how many samples are needed to create a new cluster. In the end each cluster consists of time points belonging to the same behavioural motif. Motifs are extracted from all time series using the cluster index, returned by the clustering algorithm. A motif is a series of the same predicted behavioural classes over consecutive time points. More complex motifs can be defined as repetitive,

sequential or unique patterns which can be found across the labeled instances. Such minute changes among detailed behavioral classes can then be used to determine initiation events or more precise changes in an individuals behavior.

Pairwise Analysis

Here, labeled time series were used to estimate the leader-follower dynamics of biologically relevant and highly stereotypic behaviors in fighting *P. mexicana* males. Detections were labeled at a sub-second level and grouped accordingly, resulting in highly resolved time series of behavioral classes (see Figure 25). These signals (see Figure 25) were correlated using pairwise cross-correlation (see signal.correlate in `scipy` v1.10.0) to estimate the temporal delay between the two individuals and, more specifically their behavioral display during fights. The cross-correlation resulted in a maximum correlation value and corresponding time lag for each recording of an interacting pair (see Figure 25). Timing offsets or lags between signals were then compare across the groups of winners and losers. This was done using a generalized linear mixed-effects model (GLMM) with binomial distribution family to allow for a binomial response, and to asses if the lag would signify a fight outcome (win=1, lose=0).

Behavioral Composition

The behaviors observed within a time series were quantified by presence-absence, allowing for the comparison of behavioral sequences by their pairwise Bray-Curtis dissimilarity:

$$\mathrm{BC}_{ij} = 1 - \frac{2 * C_{ij}}{S_i + S_j} \tag{6.1}$$

The Bray-Curtis dissimilarity (BC) is defined by the sum of the least abundant but shared entries across two samples i and j, divided by the sum of the total numbers of entries detected (S_i and S_j) across both sites. Therefore the dissimilarity is 0 when both sites share all species and 1 if none are common. This metric is commonly used in ecology to asses species compositions between sampling sites. Here, our sites correspond to the behavioral time series and the species are the observed behaviors. To compare the behavioral sequence of winners and loser the Bray-Curtis (see Equation 6.1) dissimilarity was calculated across all possible pairs of individuals and statistically evaluated.
How the behavioral frequency was determined by the fight outcome was tested using a linear mixed-effects model (LMM) with gaussian distribution family. This was done to account for multiple confounding variables and to test all behaviors at the same time. Manually labeled time series were each chunked into 10 samples,

where the probability of each observed behavior was calculated as the total number of observations per chunk divided by the length of the chunk. The LMM model was designed to have the behavioral probability as the response variable and time (continuous), chunk index (10 level, factor), fight outcome (2 level, factor, win=1, lose=0) and the behavioral label (12 level, factor). An interaction term was added between outcome and behavioral label to test for behavioral differences between winners and losers. To account for individual variation and consistencies across recordings individual identity was added as random effect.

All statistical analysis was done using R (v4.2.0 'Vigorous Calisthenics'), where models were constructed using the library `lme4` (v1.1-32) and best fit was established through comparison of the corrected Akaike information criterion (cAIC) (aictab, `AICcmodavg` v2.3-1). The statistical model with the lowest cAIC as well as all models within 4 ΔcAIC units are considered equally supported, while emphasis was given to models which also best represent the experimental design.

6.1.3. Results

In total eight pairs of *P. mexicana* males were tested (N=16) resulting in eight winners and eight losers. Of these 16 fish only six individuals were fully tracked and their manual and automated behavioral data collected. However, for the purely automated approach all 16 individuals were used. Overall 12 behaviors were scored manually (Appeasement, Bite, Chase, Circle, Copulation, Flight, Lift tail, Nipping, Ram, S-position, Spread fins, Tail swing) which were scored according to their description Bierbach et al. [25] and done so by D. Bierbach (description can be found in the supplemental material 1). As for the automated approach a total of 93 behaviors were categorized, by which the trajectories were labeled accordingly (see Figure 24 and 25).

Methodological Comparison

The difference between manual and automated behavioral classification is most prevailent in the number of behaviors being detected. Manually 12 behaviors were described, while the automated approach resulted in 93 individual categories (92 when excluding the class of 'unknown'). In order to determine sampling bias between both methods (manual/automated) the proportion of detected to total number of behaviors per recording was estimated. This was then correlated in order to show any sampling bias. Manual scoring detected lower proportions of behaviors compared to the automated approach, where an increase in manually scored behaviors lead to a decrease in those automatcially detected. The correlation between manual and automated was negative but not statistically significant (Spearman: r_8=-0.331,

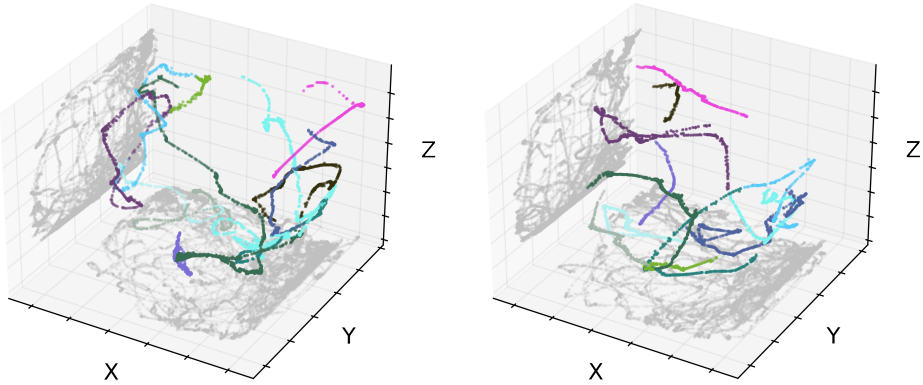

Figure 24. Trajectories of two interacting fish (left and right) over the course of 6 minutes and labeled with 12 of the most prevalent automatically determined behavioral categories out of a total of 93. Grey shadows show the extent of the full trajectory along the corresponding x-y and x-z planes

p=0.425, n-permutations: 10000; retrieved with subsequent permutation test, for correction of low sample size, Figure 26).

Behavioral Variation

The Bray-Curtis dissimilarities between both winners and losers were compared in a full factorial fashion (i.e winner-winner, winner-loser, loser-winner, loser-loser) using a Kruskal–Wallis one-way analysis of variance (scipy v1.10.0). Winners and losers were found to significantly differ in their manually observed behavioral patterns (H_1=6.51, p=0.011 *), which was not the case for the automated approach (H_1=0.178, p=0.672). By closely looking at the manual behavioral differences between winners and losers the frequency of both appeasement and flight behavior differ (see Figure 27). When examining the behavioral frequencies among the tested individuals a significant difference was only found in the probability of appeasement behavior (Appeasement: t_3=-2.660, p=0.038 *; Flight: t_3=-1, p=0.356; see Figure 27). Appeasement was then left out of subsequent analysis to determine other influential behaviors using a LMM, given that it was only observed in individuals that had lost a fight. The total explanatory power of the resulting linear mixed model was substantial (conditional R^2 = 0.61, marginal R^2 = 0.28). The interaction between fight outcome and behavior was of specific interest, where a significant positive interaction effect was only found for the spread fin behavior in winners, meaning that this behavior was observer significantly more often in winning individuals (β=0.12, CI = [0.04, 0.21], t_{940}=2.76, p=0.006 *). Further, a positive and non-significant but suggestive effect was found for the S-positioning in winners as well (β=0.08, CI = $[-4.99e-03, 0.17]$, t_{940}=1.85, p=0.065 ·).

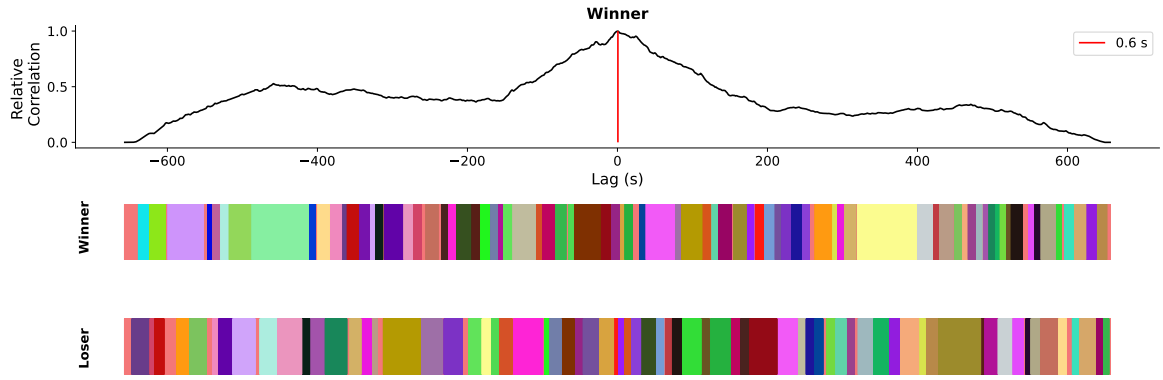

Figure 25. Cross-correlation between two behavioral time series (colored ribbons) of two individuals interacting over the course of 6 minutes. Time-series (bottom left and right) are shown below in color. Each frame is labeled with one of 25 automatically determined behavioral categories and corresponding color.

As for the automated approach, although no difference was found in the abundancies of the labeled behaviors between winners and losers (see Bray Curtis comparison above) a differences could be shown in the expression magnitude of each component. This is done by looking at the loadings for each dimension spanning the behavioral state space. In other words, each behavior is expressed by a certain composition of dimensional weights or values. The label for a given behavior may be the same and therefore the dimensions which it is comprised by, but their overall magnitude can still vary, putting each behavior on a scale from weak to strong. The twelve most predominant of the 93 behaviors labeled using the automated autoencoder were analyzed in a pairwise fashion. This was done by comparing the dimensional loading between the group of those that had won and those that had lost, where no differences were found between treatment groups and their corresponding behaviors (see Figure 28 and Appendix Table 2).

Social Interaction

To investigate the coupling between the two fighting individuals, automatically derived behavioral labels were used to compare cross-correlational time delays between interacting individuals. The automated labels were used, given that this method suggested a higher level of resolution when compared to the manual descriptions (i.e 92 vs. 12 behaviors). No significant effect of the inter-individual cross-correlation time lags was found on the outcome of a fight when comparing winners and losers using a GLMM as described above (see Section 6.1.2) (odds_{lag}= 3.067, CI = $[0.003, 2991]$, p=0.750). This means that there was no clear correlational structure that could be resolved from the behavioral time series of the interacting opponents.

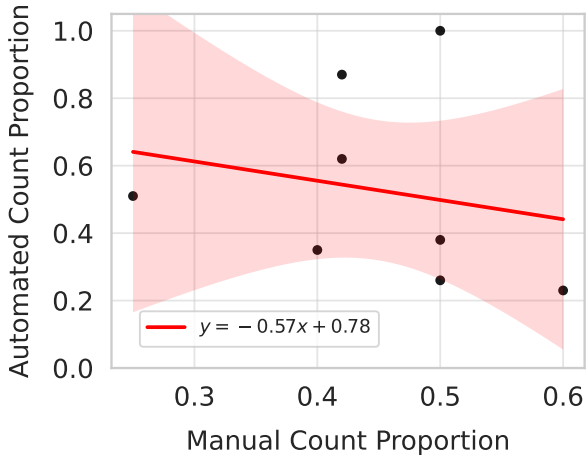

Figure 26. Correlation between the proportion of behaviors detected in a given recording to total behaviors observed across all recordings. Manual proportions are shown along the x-axis, while automatic proportions are shown on the y-axis.

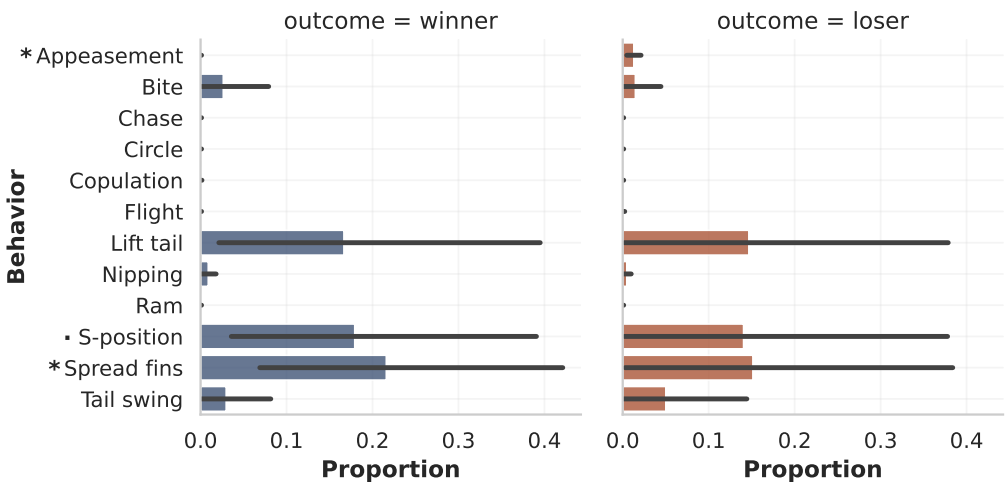

Figure 27. Histograms of the proportion of each manually observed behavior across winners (left) and losers (right). Error bars are acquired across individual recordings. Significant differences are labeled with an asterisk (*) and suggestive results with a dot (·)

6.1.4. Discussion

In this study we found that behavioral differences are found between fighting male fish, performing highly ritualized and stereotypic behaviors. These behavioral differences were evaluated both manually by using a classical ethogram and scoring

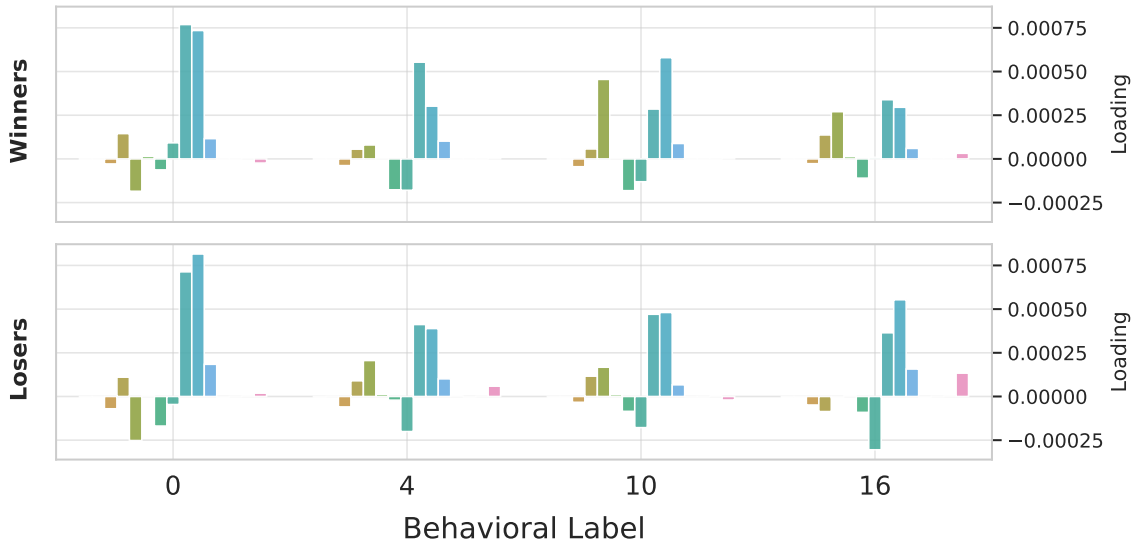

Figure 28. Example histograms of four selected behavioral clusters, as labeled by the autoencoder. Each dimension is shown as separate bar per labeled behavior along the x-axis while the corresponding loading in that dimension is given along the y-axis. Behavioral labels are separated by winners (top) and losers (bottom).

the behavioral classes, and via a unsupervised method using a trained neural network to classify the trajectories. In the latter approach the behaviors are not defined prior to the analysis but are found by spatio-temporal similarity of body positions and motion. The manual approach lead to 12 distinct behavioral classes as defined by Bierbach et al. [25], while the automated approach resulted in 93 categories. Since both approaches differ substantially in the way they classify behaviors they were compared by the proportion of behaviors detected in a given recording to the total number behaviors across all recordings. This allowed for the correlation between both methods to be established, which was negative but non-significant, meaning that detecting more behaviors manually would lead to less detection in the automated approach. The manual approach was able to distinguish differences in the behavioral repertoire expressed by the fighting individuals. It was found that losing individuals showed significantly higher proportions of appeasement behavior, while winners showed elevated sigmoid display and significantly higher amount of time displaying spread fins. The automated process on the other hand did not detect any differences among the individuals although it arguably classified the behavioral time series on a finer scale. Using the fine grained behavioral classifications the interaction among fighting individuals was further dissected. This was done using the paired cross-correlation of the time series to determine whether individuals were leading or following concerning their behavioral patterns. Here, as well no significant evidence for differences among the winners and losers was found in their temporal lag to

each other. Lastly, the automatically determined behavioral classes were compared in their fine scale composition across winners and losers to determine if minute differences between the individual behavioral classes could be found. However, here as well there was no difference between the two groups.
Overall, the here presented work shows how behavior can be quantified and compared across individuals. This study however highlights an important aspect of the development of ethology which has seen an influx in computational and quantitative tools in the recent years [33]. Quantitative tools are being applied to recover fine scale behavioral states and motifs and should be compared to the traditional approach of human observational descriptions. Manual observations have an inherent observer bias leading to difficulties when comparing behaviors across data sets or behaviors of different species. This is the main aspect unsupervised, quantitative methods as the one shown here try to address. In this work the manual observations resulted in significant insights, which does not mean that the other approach was not fruitful. The detail at which data is collected from these standardized and automated approaches is very high (see Figure 25 and 28) An explanation as of why differences were found in the manual approach but not in the automated can simply be due to the finer granularity and selection of time scales. By observing animals and classifying their behavior manually the time scale is inherently flexible and being shifted continuously. A bite behavior happens on a different time scale as an appeasement behavior, and a ram is quick while spreading the fins may take more time. An observer adjusts these time scales dynamically often without noting the difference and this has to be explicitly implemented in an algorithm to recover behaviors across such scales. In the here presented approach the various time scales were estimated using the wavelet transformation (similar to a Fourier-Transformation) of the original signal. To accommodate larger time scales, as the manual observations most likely did, the frequencies used here should likely be adjusted or a more explicit method be chosen (see Costa et al. [51]). The subsequent clustering step introduced confounding effects and biases as well such as the minimum number of clusters or the minimum number of samples per cluster. These can be adjusted and fine tuned for better results or other methods can be chosen (e.g K-Means Clustering).
Given the two ways of labeling the same behavioral time series (manual and automated) the most intuitive comparison would be to do so on a behavioral level. One behavioral class can be compared to those derived from the other method. Unfortunately this was not applicable in this case since the exact overlap between both manual and automated time series was not available.
Although the differences between both methodological approaches are apparent an interesting point of discussion is the impression that an observer may classify multiple behaviors at the same time e.g "A bite happening while having the fins spread". From the instantaneous labels of the automated output it seems as though a time point can only be labeled with a single class. The data used for the automated

analysis was derived from point detections and 3D coordinates. These are limited predictors of the actual behavioral space, given that an individual can deform its body to take on various shapes where their posture over a specific time scale defines the behavior. Therefore, although the recordings were done in three dimensions, a shortcoming of this work is the dimensionality of the behavioral space analytically observed. This can be mitigated by recording multiple body point locations or the entire body shape over time and use this as input for the subsequent classification process. Such approaches are widely used in other study species by now such as fruit flies [122] and rodents [112] while the application in fish and their intricate social behavior is still limited and is a great avenue for further work.

6.1.5. Conclusion

In the here presented work we highlight the differences between manual observations using traditional ethograms and a novel approach of quantifying behavior using neural networks trained on behavioral data. The goal was to determine behavioral differences among fighting male fish (*P.mexicana*) and highlight whether behaviors exist which predict the outcome of such an interaction. Both manual and automated approaches hold benefits and costs, as manual observations are straight forward and allow for the immediate recording of the data, while automated application remove observer bias and allow for higher levels of standardization across individuals and recordings[33]. Classical ethograms were developed to standardize observations as well, and are likely to be surpassed by algorithms performing their job. However, to put a biologically valid label on the algorithmic output a professional opinion is always needed. Therefore, only by merging both an experienced observers opinion and an unsupervised approach will behavioral classification and description be advanced.

6.2. Detection and Tracking in Convoluted Scenes

Finally, as all previous work has focused on laboratory based experiments, it remains vital to understand behavior in the natural context in which it evolved. This is especially important when investigating naturalistic behavior, where captive animals often show confounded and limited behavioral repertoires [157, 118]. To do so can be cumbersome, where bringing equipment to the field and recording data of the same quality as in the lab is often tiresome and near-impossible. However, with the help of computerized methods, such as object detection and tracking using artificial intelligence, drones and computer vision, highly resolved data can be acquired in the natural terrain [66, 123]. The main goal of the following work was to bridge the fields of computer vision and biology further, and achieve similar results as Koger

et al. [123] but in the open ocean. Most importantly, such approaches need to be easy to use, in order to allow researchers to acquire data from field recordings and speed up the process of hypothesis testing.

6.2.1. Introduction

Ethology and the study of animal behavior often faces the problem of restricting the subjects behavior in order to achieve measurable outcomes, while simultaneously trying to minimize all confining factors of naturalistic behavior [118, 219]. Undeniably the most naturalistic behavior can only be observed in nature itself, where animals are interacting with, and responding to the environment in which they evolved in. While naturalistic scenes can be replicated in a laboratory setting animals can be tagged or tracked directly in the wild using a multitude of methods ranging from GPS, RFID and accelerometer tags [116], to arguably less invasive image based approaches using drones and cameras [66, 123]. Drone based approaches as those applied by Koger et al. [123] are appropriate for terrestrial terrain, where the abundance of terrain features allow for the camera location to be accurately estimated. In the open ocean this is not so easy, since reliable and fixed environmental features are sparse or absent. Image based approaches have gained popularity, aided by the fact that detection and tracking algorithms have greatly improved within the last decade and it is now possible to consistently identify and track individuals in various terrains and environments [152, 66, 230, 123, 171]. An advancement which has lead to great improvement in these techniques is the implementation of artificial neural networks which are capable of learning to segment out region of interest and distinguish these from the background. These networks are commonly trained on a subset of the data where the objects of interest are annotated and classified manually. Once trained the networks, also referred to as models, can be used to make predictions on novel images. The form of annotation somewhat defines the data which can be learned and prediction output format, where a variety of methods exists. For example, the entire image can be classified depending on what object is visible in the scene where an image containing a cat could be classified as "cat". However, this approach does not us to determine the exact position of the object in the image. Therefore a finer scale can be applied in which a bounding box is drawn around the object of interest, commonly resulting in a representation defining the box and a label. A similar but more detailed approach is the segmentation mask, which is drawn around the object of interest and represents a polygon with approximately the shape of the object and a label. Lastly, the finest scale which is achieved is by annotating individual points in the image. These are commonly called key point annotations and can be used to estimate body part locations and subsequent pose.
Today the technical innovations and field based approaches are coming together leading to interdisciplinary work and opportunities which pave the way for highly

detailed and unprecedented insights into the live of animals in the wild [116, 212, 66, 123]. The goal of the here presented work was to minimize the gap between innovation and application and create a streamlined, easy-to-use approach for quickly testing and retrieving data from complicated scenes in the wild. To do so the object detection and scene segmentation network Detectron2 was used, which was developed by Meta Open Source [243]. It was applied to video footage of striped marlin *Kajikia audax* aggregations predating schools of sardines *Sardinops sagax* in open water of the coast of Mexico. The predatory groups hunt down the schools of prey and collectively diminish these, subsequently referred to as bait balls, over the course of the day [84]. The material incorporated both overhead drone and underwater recordings and therefore represents a multi-angle representation of the objects of interest. Detections were subsequently tracked using the openly available NORFAIR library. In order to make the entire process of custom annotation, model training, prediction, tracking and data retrieval as simple as possible it was incorporated into a single pipeline using all open source applications. These were further simplified by creating simple user interfaces (Python library Gooey). This allowed for user friendly, single click applications, in which the user can select all options manually and is guided through the process without the need to interact with any raw code.

6.2.2. Methods

Beginning from raw video material a total of 200 annotation images were randomly selected from the video frames using the freely available, command line tool ffmpeg. Other options exist using optical flow or clustering to retrieve maximally different images, but for simplicity random selection was sufficient in this case. Four classes of objects (Human, Sealion, Marlin, Bait Ball) were annotated as segmentation masks in all images using the online tool makesense.ai and exported in the Common Object in Context (COCO) format. The segmentation mask is an outline drawn around an object, and allows for the object's center (in form of Euclidean coordinates) and the shape of the object's outline to be analyzed. A default model architecture (pretrained mask_rcnn_X_101_32x8d_FPN_3x), training schedule and settings were then used to train a network on these annotations (92 annotated images, 4 classes, 500 warm-up iterations, learning rate: 0.00025, 100000 iterations). Training was done on a consumer grade GPU (NVIDIA Quadro RTX 4000) and took roughly 48 hours. Once sufficiently trained, the model was used to predict on entire videos from both top-down and side view observations, of hunting events. The predictions returned are in form of binary pixel based masks for each detection. For example, in a frame in which there is a marlin and a bait ball visible, the model would likely give two prediction images (masks) with the same dimensions as the input image, where pixel are encoded as 1 if they are predicted to belong to the corresponding class and 0 if

not. Each prediction further is associated with a probability score, representing the confidence with which the given class is detected by the model. Predictions were then passed through the NORFAIR algorithm to obtain semi-continuous tracks, with consistent identities of the individual detections over time.
All detections are frame-wise, pixel based and commonly refined to a row corresponding to an object's center coordinates (x, y), time stamp (frames), class label and prediction confidence score. In order to retrieve real world coordinates and derived values such as longitude and latitude and distances in meters the images need to be references to a global coordinate system. This system is provided by the onboard GPS system of the drone which collected the images and allows for the images to be back-transformed, similar to the procedure shown in Francisco et al. [66]. The movement of the drone, or image capturing device needs to be removed from each trajectory in order for the actual position and subsequent speed to be calculated. This step of the process is similar to the work done by Koger et al. [123], but was not part of the here presented work and is yet ongoing.

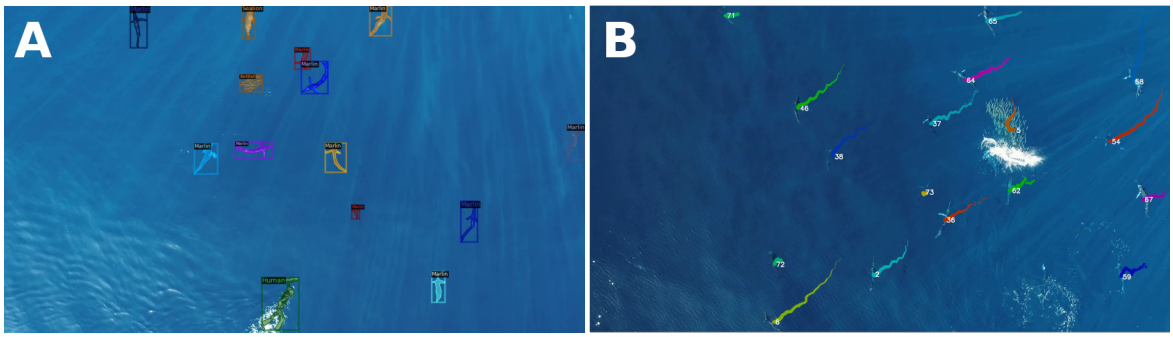

Figure 29. Example visualization of output retrieved from model predictions. **A** Mask based object detection results, **B** tracking result of the frame-wise detections over time shown with trailing trajectories

6.2.3. Results

The entire workflow was broken down into easily executable, smaller steps and incorporated into a interactive notebook (Jupyter Notebook). Further, a user interface (GUI, using Gooey) was developed for each of the individual modules for increased utility and a user-friendly experience. As for the preliminary data, the resulting trajectories of both predators and prey were used to calculate descriptive statistics and relevant values such as the inter-individual distance and distance between predators and prey. Given that the coordinates were not transformed into real world coordinates all measurements are in pixels. Further, given that the motion and momentary height of the camera was not compensated for in this work, only relative distances in pixel values between objects could be established (see Figure 31). These

results only highlight the further possibilities which can be achieved with the here presented methods.

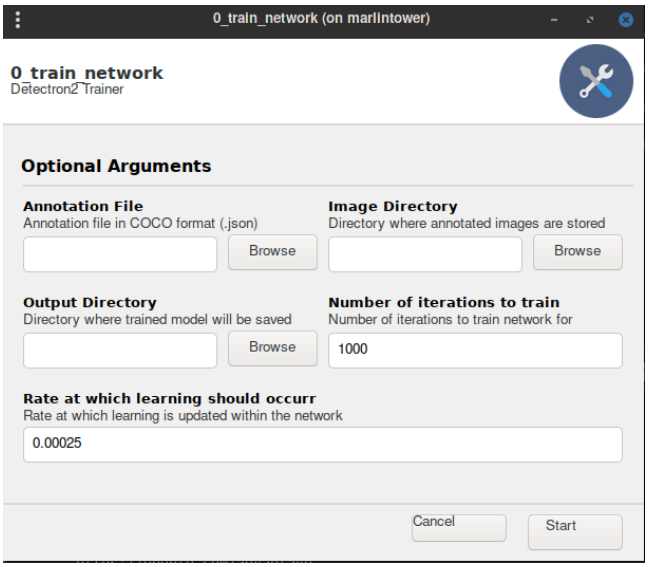

Figure 30. Example showing the user interface (GUI) developed to make the training of the classification network easier and more user-friendly

6.2.4. Discussion

Computer assisted methods for object detection and tracking have led to substantial advances in the study of animal behavior [212, 33, 66, 123] and these benefits have been highlighted with this work. A goal of the here presented simplified approach is to make the process of object detection and tracking more user friendly and streamlined allowing researchers to spend less time working on the methodology and enable them to dive directly into collecting data and testing their hypotheses. A main aspect of streamlining such approaches was to make it customizable for various conditions and questions, such as varying image quality and viewing angles, different object classes of interest and occlusions. Further, it was emphasized in this methodology to only use freely available and open-source software. This was done to remove limitations due to financial constraints and paywalls which some may face during their work. From a biological point of view the main insight and gain from these methods is the fact that they enable behavioral observations to be done on a high spatio-temporal resolution, across multiple individuals and species. Interdisciplinary approaches as these are important to push the boundaries of what individual research fields can achieve and lead to innovation across them. A limitation which is always at play is the expert knowledge of researchers in one field which is not always easily shared all members of a research group or

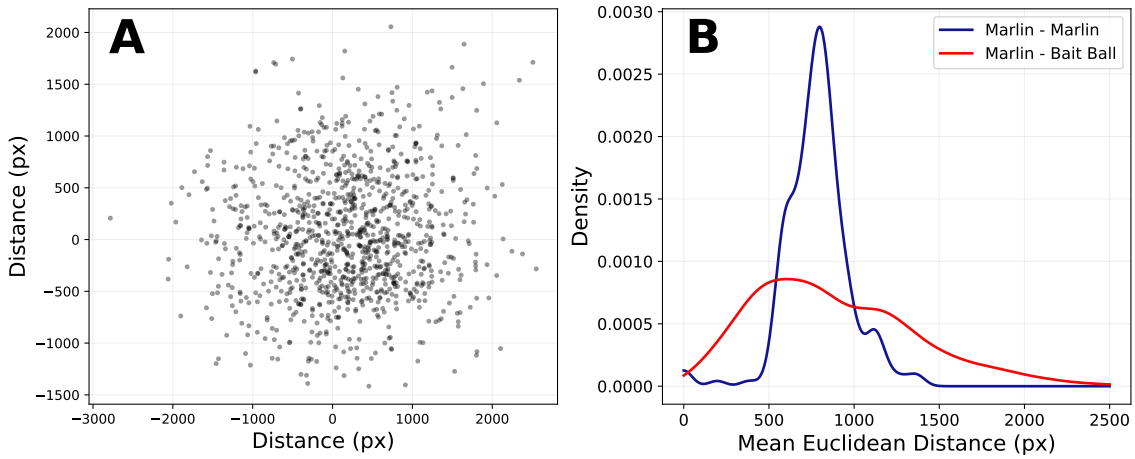

Figure 31. Visualization showing the cumulated data of a total of 14 recordings **A** distance in pixels between predator (marlin) and prey (Bait Ball), **B** Distribution of interindividual distances between predators (blue) and their distance to the prey (red)

community. Therefore a common ground needs to be established from which to work from. Further, although object detection has made great advance in recent years the consistent tracking of such objects leading to individual based trajectories is still lagging behind and is only slowly catching up [230]. While trajectories which are not individually corrected can be useful for relative measures, such as nearest neighbor distances, or to calculate distances between predator and prey they do not allow for precise estimation of individual behavior and subsequent responses.
The ability to observe undisturbed multi-species communities and predator-prey interactions in their natural habitat is groundbreaking. These methodological advances have the potential to enable a flood of innovative and long standing biological questions to be addressed. It is not unlikely that the resolution of prey behavior can further be advanced as well by which minute individual behaviors and their outcome can be studied (i.e. "turning away from the rest of the school in a certain moment and the resulting likelihood of being eate"). In the case shown here the bait ball can be detected in each frame in which it is visible in and subsequently cropped out and enlarged. In a second pass individual sardines could be detected within the bait ball, movement of pixels can be estimated through optical flow to determine whether self-sorting processes are in place or the shape of the school can be analysed in more detail in response to increased risk or predation.

6.2.5. Conclusion

The here presented methods are advancing quickly and continuously becoming replaced by newer, faster and more precise approaches. However, the implementation in applied fields such as behavioral research is often lagging behind, which is often

due to little convergence or interdisciplinary exchange. Here, the approach was taken to bridge this gap and create a link between the fields of computer vision, machine learning and ethology. Overall these approaches are continuously necessary to join innovation with application. Expertise from various fields must be coupled by which researchers must reach a common ground to work from. The study of animal behavior is a perfect conjuncture allowing for such interdisciplinary work to take place and lead to groundbreaking new insights. The main innovation being, that these approaches continuously enable wild animals to be studied in their natural and unconstrained environment in which they have evolved at a precision of lab based approaches [212, 66, 123]. In order to reduce redundancies among scientific fields the exchange of expertise and knowledge is needed. This is not only needed on a conceptual level where ideas and theories align but also on the level of individual research endeavors and scientific teams. As the complexity of most modern sciences increases the most productive teams grow in size and interdisciplinary breadth which is a necessity for tackling these complex biological research questions as well [242, 48].

7. Discussion

The variation in research topics and approaches shown in this piece of work highlights the complexity of understanding behavior and learning in a dynamic and adaptable way. Starting by elucidating the concept of learning in the genetically identical, freshwater fish species the Amazon molly *P. formosa* individual and social aspects of behavior and learning were investigated. By pairing individuals that were previously experienced or un-experienced gradients of information in a task proficiency were created within such a social pair. The effect of such gradient on the subsequent task performance was evaluated to disentangle change in performance with prior knowledge. As a result, it was found that the individuals could be trained on a classical operant conditioning task and consistently differed in their learning ability. Further, the presence of previously experienced individuals hindered those un-experienced in performing the task themselves. This effect was not found when the information gradient was not present i.e. in cases where both partners had the same prior information and experience.

Following this analysis of individual and social learning the attention was shifted towards social contagion of behavior in larger groups and the effect of familiarity among individuals on such behavior. Here the naturally occurring jumping behavior was investigated in groups (N=2,4,8,16,32) of the same clonal fish species as mentioned before, where all individuals are genetically identical. Individuals were found to perform evasive jumping behavior in all group sizes. Familiarity was tested in pairs of unfamiliar and familiar individuals where their individual probability to jump was determined. Familiarity was found to have an effect on the waiting time before jumps were initiated, suggesting that social partners can effect such behavior. Further, in larger groups the social contagion of jumping behavior was tested and it was found that this behavior is in fact socially influenced, as the spatial and temporal distributions of individual jumps were significantly non-random. Inter-jump intervals in time and space were shifted towards smaller values, when compared to random samples suggesting a form of social coupling taking place.

These social aspects of behavior as well as their temporal change over time and adaptation to various aspects of the environment were then tested in the subsequent analysis of behavioral variation in isolation and within a social context. Again, the clonal Amazon mollies were used as model organism and grouped into social groups of four size matched individuals. To estimate the variation in individual behavior individuals were repeatedly tested in isolation and subsequently in a social context, where the median speed was used as behavioral proxy. Environmental complexity was altered by adding visual occlusions through structural barriers to

add a non-social aspect of adaptation. As a result no correlation between individually acquired behavior and that observed in a social context was found. In isolation individuals showed no consistent individual differences in their swimming speed, while this was the case over all observations within the social group. Overall, it was found that the social context, physical environment, as well as habituation time had an effect on the behavior in these fish.
Behavioral adaptation to food availability was tested given that metabolic state, as well as the energetic requirements and the availability of prey are drivers of behavioral variability. Clonal fish were separated across three feeding regimes receiving either conventional food, live prey or immobile prey. The growth rates and behavioral response in form of median swimming speed were recorded over the course of 40 days. The main results suggest that while feeding regime had an effect on the growth rate it did not effect the swimming performance. Further, the variability in prey density did not predict the variation in swimming performance, showing that no behavioral adaptation was observed over the course of the experiments.
Behavioral adaptation was further investigated at a higher spatio-temporal resolution and by comparing behavioral annotations done by an expert observer and those acquired through a trained artificial neural network. By doing so both methodological approaches were compared and behavioral differences between individuals, as well as their effect during competitive interactions were evaluated. Here, it was shown that manual observations allow for a distinction between winners and losers of an agonistic interaction, while automatic approaches failed to do so. The difference between partners was found mainly in the frequencies of specific behaviors. Although the automated falls short to give insightful results, these methodological advances gives way for promising new avenues to continuously map behaviors onto a common landscape of actions.
As approaches for quantifying behavioral changes improve for the lab based research, the same can be applied to data acquired in the field. Behavior can then be studied under all the natural constraints in order to test long standing questions of social aggregates, predator and prey interaction and collective behavior. Field data is commonly noisy and inaccurate given that controls can't be accounted for and standardization is often impossible. However, by utilizing high speed cameras, aerial and submersible drones, as well as artificial neural networks, a high level of precision can yet be achieved. In the here presented collaborative project a custom object detection and tracking pipeline was developed to acquire data from pelagic predators collectively hunting small schooling prey in the open ocean. In a short application, the inter-individual distances between predators, as well as between predator and prey were established from the obtained trajectories.

From much of the existing research on learning and learning theory it becomes clear that the learning process highly depends on the situation and context in which it

evolved in or was necessary. This has led to a great plethora of learning studies with divergent and congruent results across various taxa making it somewhat hard to distill the overarching concept. Although this was not even remotely the goal of this study, reading through some of the vast literature was a requirement to gain any traction. The field of learning theory and animal learning is vast and has resulted in many such examples of learning processes and mechanisms, while the research attempts with focus on the processes involving collective learning have been limited. This is likely due to the fact that collectives are harder to study in general, and especially over longer periods of time and at high resolution (although not impossible, see Wild et al. [238]). Fewer individuals are more readily accessible and can be followed or tracked more easily. Advanced studies are necessary to shed light on the processes governing adaptation and learning in groups of individuals and multi-agent systems, especially focusing on the collective identity and the effect of group size and individual heterogeneity [120, 111]. This not only allows for fascinating discoveries in non-human animals, but can also have implications for our own, everyday behavior as humans. For example, work on the behavior of humans online and the spread of information and/or misinformation is highly relevant for managing emergency situations or distributing knowledge [89]. Much of such work is motivated by research on non-human systems, such as that by Couzin and Krause [53] and Rosenthal et al. [190]. The direct link between such work is the study of complex systems which acts as a unifying concept that can be addressed from many angles. Throughout the here presented work, finding a unifying concept has been a fundamental aspect of interdisciplinary collaboration and can be put forth as further finding. From the experience gained in this work, high intellectual and scientific return can be expected when distant fields, such as computer science and ethology or physics and evolution come together and find a underlying, common principle in their work.

A similar connection which is vital in biological experimentation is the bridge between lab and field based observations. Although the information gained from lab based approaches is limited, it allows for highly controlled and standardized approaches. Field approaches contrast this by being highly complex and subject to high variation, often making experimentation more challenging. Experiments in both lab and field are therefore highly valuable to understand natural processes and systems in their relevant context [45]. Many if not all such processes in nature are time dependent and transient, as behavior is as well [20]. The detailed analysis of behavioral development over time allows for the probability distribution of applied motor commands to be estimated and the informational gain to be compared to previous and future states [44, 245]. By coupling long-term observations over developmental time scales with such quantification methods, the development not only of the animal but of the behavioral patterns exhibited can now be studied comparatively [168]. Such approaches are vital in understanding the utility of behavior, as well as it's adaptations and structure [21]. The underlying decision-making processes in individuals and collectives alike can be studied similarly by observing multiple individuals interacting and assessing their behavioral changes [122, 3]. As our societies and close nit circles of friends effect our own actions and decisions on a daily basis the difference among opinions we perceive and the behavior of those closest to us changes the way we behave [64]. From non-human

animal behavior to our own, insights gained from the field of ethology can often be generalized and lead to humans fundamentally rethinking how they act as a people [127, 145].

When recapitulating the overall findings shown here a coherent theme is the fact that behavior, as well as learning takes place on various time scales and is highly dynamic and context dependent. This has been shown to be true for behavioral variation in response to environmental complexity [5] and overall learning in animals [220]. Information is integrated over time and in turn leads to a change in behavior, while behaviors can be adapted to a certain situation or based on a internal state at a specific moment in time. Experiments and methods as those shown here are crucial for understanding the mechanisms that shape behavioral development and learning over time. Following Hartmann [87] time, space and the corresponding action taken in form of behavior, give insights into the underlying processes and beliefs being processed in the brain. This gives rise to a multitude of questions concerning the effect of sequential experience on behavior and behavior as a context dependent, generative process which produces information.

On a broader scale, seeing our species and the complex interactions as a dynamical system and understanding the behavioral processes driving it further allows us to determine mechanisms to avoid misinformation and help make changes required to achieve a more sustainable, fair and healthy society [89, 224, 145]. Little is know about the evolutionary background of behavioral heterogeneity in biological communities and the potential benefits and costs associated with such and holds many promising results still to be uncovered [90, 104, 139]. In a sense of community and following what we know so far, discussions should be fostered and opinions ubiquitously voiced, in order to remove barriers and undermine inequalities [241, 17, 145].

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9. Contributions

Doctoral Regulations of the Faculty of Mathematics and Natural Sciences, published in the Official Gazette of the HU No. 42/2018 on 11.07.2018.

Declaration according to § 7 para. 5 b (Monography)

1. Family Name, Name : **Francisco, Fritz A.**
   PhD Subject: **Biology**
   Title of the dissertation: **Adaptation and Learning in Fish: Effect of individual behavioral and informational variation on collective outcomes**

2. Numbered list of publications/texts/results:

   2.1. Experienced social partners hinder learning performance in naive clonal fish, F. A. Francisco, J. Lukas, A. Stöcker, P. Romanczuk, D. Bierbach, bioRxiv, October 17, 2022

   2.2. Collectively induced jumping behaviour in a clonal live bearing fish, F. A. Francisco, A. L. Kesim, D. Bierbach, P. Romanczuk, *in prep.*

   2.3. Behavioral variability as response to reduced uncertainty in a clonal fish, F. A. Francisco, L. Gomez, A. Escurra, C. Schutz, P. Romanczuk, D. Bierbach, *in prep.*

   2.4. The effect food availability and motility on the swimming behavior and growth of the clonal fish *Poecilia formosa*, F. A. Francisco, C. Schutz, P. Romanczuk, D. Bierbach, *in prep.*

   2.5. Quantification of highly stereotypic fights in a live bearing fish using manual and automated approaches, F. A. Francisco, L. Skopeteas, L. Gomez, P. Romanczuk, D. Bierbach, *in prep.*

   2.6. The dynamics of predator-Prey interactions and collective hunting in the open ocean, M. Hansen & A. Burns, F. A. Francisco, K. Pacher, J. Krause, *in prep.*

3. Presentation of the own share of the publications/texts/results mentioned under point 2 and their connection with parts of the dissertation:

   3.1. The author of this thesis developed the hypothesis and experimental design together with David Bierbach and Pawel Romanczuk. The complete infrastructure (tracking software, experimental setup, multi camera streaming pipeline etc.) was created by the author. Experiments and the pre-analysis were conducted by the author and students under his direct supervision (Jakob Soelter, Alessandra Escurra, Leonidas Skopeteas). The statistical analysis was performed by the author together with Juliane Lukas, David Bierbach and Almond Stöcker. The author composed the text which was reviewed and approved by all contributing authors.

   3.2. The research idea was developed together with David Bierbach, while the author conducted the experiments and group level analysis. Data recorded from pairs of fish was recorded by Ayla Kesim as part of an internship under the supervision

of both David Bierbach and the author. David Bierbach performed the pair-wise interaction and familiarity analysis, which was reviewed and reproduced by the author. All subsequent analysis, data revisions and modeling aspects were done by the author. Supervision and feedback on the specifics of modeling was given by Pawel Romanczuk. All authors contributed to writing and reviewing of the corresponding manuscript.

3.3. Both the research idea and experimental design were developed by the author in exchange with David Bierbach and Pawel Romanczuk. The experiments were conducted by Alessandra Escurra under supervision of the author, as part of her Master's degree. Pre-processing of the data was done by Alessandra Escurra, Christopher Schutz, Phoebe Schladitz and the author, where the author performed the final post-processing steps. Subsequent analysis and statistical testing was done by the author.

3.4. The research idea, hypothesis, and experimental design was developed by the author together with Christopher Schutz. All required coding, pre-processing analysis and statistical modeling was done by the author, while the experiments were conducted by Christopher Schutz under direct supervision of the author. Development of the software for standardized, automatic measuring of fish was done by David James, David Bierbach and the author. Implementation of the program was predominantly done by David James under supervision of David Bierbach and the author. Further support was given by Pawel Romanczuk and David Bierbach towards the behavioral evaluation and experimental design.

3.5. The research idea, hypothesis and experimental design was developed by author together with David Bierbach, Pawel Romanczuk, Luis Gomez and Leonidas Skopeteas, as part of the Bachelor's thesis of Leonidas Skopeteas. Experiments were implemented by the author together with Leonidas Skopeteas and conducted by Leonidas Skopeteas under direct supervision of the author and L. Gomez. Data post-processing, tracking and preliminary analysis as part of the Bachelor's thesis was done by Leonidas Skopeteas, while the refinement was performed by Leonidas Gomez and the author. Automatic behavioral quantification and the required coding was solely performed by the author, while the manual scoring was performed both by Leonidas Skopeteas and David Bierbach. All results were cumulated, refined and visualized by the author. All authors contributed to writing and reviewing of the corresponding manuscript.

3.6. Research hypothesis and scientific approach were developed by Jens Krause, Matthew James Hansen, Korbinian Pacher, Palina Bartashevich and Alicia Burns. Application of the detection and tracking algorithms, their custom implementation and the creation of user interfaces was done by the author, in close collaboration with all project members. All preliminary analysis as shown here was done by the author.

4. Date, Signature of the applicant

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5. Confirmation by the supervisor

I confirm the declaration of contribution handed in by Mr. Fritz Francisco according to pt. 3:

Name: Pawel Romanczuk Signature:.....

A. Appendix

A.1. Supplemental Material

Behavior	Description
Ram	First attack was categorized as a ram. Pushes at the end of a fight, are categorized as rams.
Bite	Attacks subsequent to the first ram are categorized as bites
Flight	One individual clearly fleeing from the other
Chase	An individual chasing another
Appeasement	Fish facing upwards with fins folded
Lift Tail	One fish is facing downwards while the other has only its tail lifted upwards
S-position	Fish clearly bent in a Sigmoid shaped position
Circle	Fish circling each other. Behavior usually performed by both individuals simultaneously
Tail Swing	Swing with the tail directed towards the opponent

Table 1. Ethogram as described and used by D. Bierbach

Behavioral Label	df	t-value	p-value
0	14	1.633	0.125
1	14	-0.027	0.979
2	14	-0.435	0.670
4	14	-0.154	0.880
5	14	0.674	0.512
8	14	0.366	0.720
10	14	0.528	0.606
12	14	0.231	0.821
14	14	-0.518	0.613
16	14	1.145	0.271
19	14	-0.942	0.362
20	14	-0.687	0.503

Table 2. Overview of the results of paired t-test between winners and losers across the 15 dimensions of the behavioral labels.

A.2. Glossary

artificial neural networks Inspired by natural brains, a artificial neural network (ANN) is composed of single neurons or nodes connected through synapses or edges and

	Successfully solved task without Social Context		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.11	0.06 – 0.21	**<0.001**
Trained [True]	1.55	0.67 – 3.56	0.302
Time since solved	0.87	0.71 – 1.07	0.180
Trained [True] × Time since solved	3.93	1.83 – 8.45	**<0.001**
Random Effects			
σ^2	3.29		
$\tau_{00\ \mathrm{ID}}$	0.19		
$\tau_{11\ \mathrm{ID\ Trained:Time\ since\ solved}}$	0.55		
$\rho_{01\ \mathrm{ID}}$	1.00		
ICC	0.06		
N_{ID}	36		
Observations	450		
Marginal R^2 / Conditional R^2	0.830 / 0.839		

Table 3. Model summary for the estimation of the effect of training on the success of solving the task in an individual setting without social partner. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

commonly structured in layers. It receives input and processes it by which the nodes and edges are weighted.

auto-shaping A form of conditioning in which reinforcement following a stimulus leads to the performance of task irrelevant behaviour (similar to superstition) [37].

autoencoder An artificial neural network commonly used to learn higher level representation or encoding of unlabeled data. This corresponds to a form of dimensionality reduction, where the input dimension is reduced to the smallest layer of the network. Autoencoders can be used for classification problems and are inherently generative models, which can generate new data similar to its input..

classical conditioning A simple form of associative learning, also known as Pavlovian or respondent conditioning, developed by I. Pavlov and J. Watson [170, 232]. During classical conditioning, an unconditioned stimulus which under normal circumstances creates an unconditioned response is coupled with a neutral stimulus. By doing so the neutral stimulus becomes a conditional stimulus and the unconditioned response becomes a conditioned response.

collective identity According to Melucci et al. [155] and Kilgore [120] the collective identity is a common understanding of 'ends, means and field of actions', shared among all members of the collective and giving a sense of 'continuity and permanence'. Analogous to Hartmann [87], the collective can here be seen as a system performing an action, according to its goal setting, choice of means and realization.

	Successfully solved task with Social Context		
Predictors	*Odds Ratios*	*CI*	*p*
(Intercept)	0.07	0.02 – 0.25	**<0.001**
Treatment [NT]	0.39	0.04 – 4.04	0.432
Treatment [TN]	24.74	2.82 – 216.76	**0.004**
Treatment [TT]	22.74	4.00 – 129.19	**<0.001**
Time since solved	7.59	3.13 – 18.43	**<0.001**
Treatment [NT] × Time since solved	0.17	0.05 – 0.57	**0.004**
Treatment [TN] × Time since solved	0.45	0.11 – 1.81	0.262
Treatment [TT] × Time since solved	0.39	0.11 – 1.33	**0.134**
Random Effects			
σ^2	3.29		
$\tau_{00\ \mathrm{ID}}$	3.21		
$\tau_{11\ \mathrm{ID\ Time\ since\ solved}}$	0.21		
$\rho_{01\ \mathrm{ID}}$	0.02		
ICC	0.66		
N_{ID}	36		
Observations	520		
Marginal R^2 / Conditional R^2	0.716 / 0.903		

Table 4. Model summary for the estimation of the effect of training on the success of solving the task in an individual setting with a social partner. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

	Individual Median Speed without Social Context (cm/s)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.52	0.36 – 0.68	**<0.001**
Date	-0.03	-0.08 – 0.03	**0.369**
Individual Size (cm)	-0.01	-0.05 – 0.03	0.734
Random Effects			
σ^2	0.14		
$\tau_{00\ ID}$	0.01		
ICC	0.06		
N_{ID}	88		
Observations	260		
Marginal R_2 / Conditional R_2	0.003 / 0.063		

Table 5. Model summary for the estimation of the effect of individual traits and environmental factors on the median swimming speed of individuals alone and without any social context. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

collective learning When conceptualizing a group of agents itself as a learning entity, the process by which this entity learns would then be considered collective learning according to Kasl et al. [113]. However, the distinction between individual contribution and group contribution when focusing on learning is harder to make and deserves special attention [120].

correlated cue Accessible to many simultaneously, leading to redundant information given that the same information is distributed across multiple receivers. This form of information has lower variance within the information quality and high correlation among receivers.

culture According to Galef [72] and Whiten et al. [237] culture (often referred to as *tradition* in ethology) is a process involving socially learnt behaviours and inter-generational transmission of information.

darwinian fitness Increased Darwinian fitness of an individual is defined as the ability to pass on more of ones own genetic material to the next generation. Commonly this is associated with having more offspring.

generalized linear mixed-effects model The generalized linear mixed-effects model is an extension of the linear mixed-effects model. Most importantly it allows for the response to be connected to the linear model through a link function.

GPS Global Positioning System.

GUI A Graphical User Interface is a platform which allows the user to interact with a program visually without the need for command line input or other means of code execution. The alternative is the Command Line Interface (CLI), which allows the user to interact with a program directly from the terminal or command line prompt.

	Individual Median Speed with Social Context (cm/s)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.49	0.17 – 0.81	**0.003**
Date	-0.01	-0.01 – -0.00	**<0.001**
Individual Speed (BL/s)	-0.07	-0.35 – 0.21	0.623
Individual Size (cm)	0.01	-0.12 – 0.13	0.930
Environment [Simple]	0.08	0.06 – 0.09	**<0.001**
Random Effects			
σ^2	0.01		
$\tau_{00\ ID}$	0.01		
ICC	0.42		
N_{ID}	72		
Observations	536		
Marginal R^2 / Conditional R^2	0.236 / 0.555		

Table 6. Model summary for the estimation of the effect of individual traits and environmental factors on the individual median swimming speed in the social context. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

imitation There are two aspects which can be generalized as being part of *imitation*: 1) *matched-dependent*, where a demonstrator can read relevant, environmental cues and act upon these, while the follower cannot and 2) *copying* where a copying individual iteratively repeats an action to match an observed action. This requires the individual to be capable of estimating its own performance [158].

individual learning The process by which an individual acquires information by interacting with its environment in absence of any social context [95, 96, 29].

linear mixed-effects model Linear mixed-effects model of linear mixed models an extended form of a simple linear model which allow for the incorporation of fixed and random effects. These are especially of interest when there is non independence in the data. These are commonly found in hierarchical or nested data structure such as individuals within groups..

local enhancement Being in proximity to a certain location, situation, event, or individual can effect the future performance based on this experience, which is referred to as being local enhancement. For example, following successful conspecifics can lead to better mate choice preferences via local enhancement and eavesdropping [235].

operant conditioning A simple form of associative learning, also known as instrumental conditioning and mainly accredited to the findings of B.F Skinner [203] and based on Thorndike's law of effect [217]. Similar to classical conditioning unconditioned responses are coupled with neutral stimuli. However, the difference here being, that the neutral stimulus elicits a positive or negative consequence, which reinforces the association.

	Group Median Speed (cm/s)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.42	0.10 - 0.73	**0.010**
Date	-0.01	-0.01 – -0.00	**<0.001**
Individual Speed (BL/s)	-0.10	-0.38 – 0.18	0.484
Individual Size (cm)	0.04	-0.09 – 0.16	0.574
Environment [Simple]	0.08	0.07 – 0.09	**<0.001**
Random Effects			
σ^2	0.01		
$\tau_{00\ ID}$	0.00		
ICC	0.42		
N_{ID}	72		
Observations	536		
Marginal R^2 / Conditional R^2	0.246 / 0.563		

Table 7. Model summary for the estimation of the effect of individual traits and environmental factors on the group median swimming speed. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

overshadowing According to the American Psychological Association overshadowing is "in classical conditioning, a decrease in conditioning with one conditioned stimulus because of the presence of another conditioned stimulus. Usually a stronger stimulus will overshadow a weaker stimulus.".

posture The instantaneous pose or posture of an animal can be seen as a specific configuration of body points and their orientation to each other (2D or 3D). Posture observed over time results in behavioral units, which in turn can make up a behavioral sequence. It is important to note that posture does not contain any temporal information, as it is a snap-shot or still image taken in time.

private information Information which is acquired individually, in absence of others.

public information Information which is accessible and acquired by many individuals. Cues leading to this form of information can further be categorized into high correlation cue (all individuals receive very similar information) and low correlation cue (all individuals receive highly variable information) [111].

RFID Radio-frequency identification used for Telemetry.

social facilitation Describes the circumstances under which a process, such as learning is facilitated by the mere presence of others [244].

social learning The process by which an individual interacts with its environment and acquires information purely through social contact.

	Individual Median Speed (cm/s)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.02	-0.53 – 0.49	**0.943**
Initial Size (mm)	0.51	0.29 – 0.73	**<0.001**
Recording Index	-0.03	-0.04 – -0.02	**<0.001**
Treatment [Conventional Food]	0.04	-0.12 – 0.20	0.629
Treatment [Live Prey]	0.08	-0.08 – 0.24	0.343
Random Effects			
σ^2	0.19		
$\tau_{00\ ID}$	0.01		
ICC	0.06		
N_{ID}	56		
Observations	206		
Marginal R^2 / Conditional R^2	0.273 / 0.314		

Table 8. Model summary for the estimation of the effect of feeding regime and total length on the individual median swimming speed. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

	Individual Median Speed (cm/s)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	-0.32	-1.06 – 0.41	**0.387**
Initial Size (mm)	0.68	0.37 – 0.99	**<0.001**
Treatment [Live Prey]	0.08	-0.10 – 0.26	**0.356**
Recording Index	-0.03	-0.04 – -0.02	**<0.001**
Prey Density (N)	-0.00	-0.00 – 0.00	0.745
Random Effects			
σ^2	0.21		
$\tau_{00\ ID}$	0.02		
ICC	0.08		
N_{ID}	37		
Observations	134		
Marginal R^2 / Conditional R^2	0.319 / 0.370		

Table 9. Model summary for the estimation of the effect of feeding regime, prey count and total length on the individual median swimming speed. Statistically significant values are highlighted with bold font. Results table was generated in R using sjPlot v2.8.14 and lme4 v1.1-32

theory of mind Theory of Mind (ToM), often described as mind-reading, mentalizing, mental-state attribution, and perspective-taking. ToM conceptualizes the process by which mental states are ascribed to others in order to understand their actions better [69]. It can be extended to where external processes, concepts and objects are mentalized in order to predict future outcomes and behaviours [128].

uncorrelated cue Accessible to single receivers at a time, leading ambiguous information among all receivers. This form of information inherently has a higher variability within the information quality and low correlation among receivers.

Selbständigkeitserklärung

gemäß Promotionsordnung vom 5. März 2015

Ich erkläre, dass ich die Dissertation selbständig und nur unter Verwendung der von mir gemäß der Promotionsordnung der Lebenswissenschaftlichen Fakultät der Humboldt-Universität zu Berlin vom 5. März 2015 angegebenen Hilfsmittel angefertigt habe.

Datum

Unterschrift: Fritz Alexander Francisco