



Final report

**“Ecological consequences of  
fish behavioural types”**

Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB)  
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## Executive summary

Behavioural types (i.e. behavioural differences between individuals from the same population that are consistent over time and correlated across different contexts) are considered to be a topic of prime importance in ecology, evolution and management. While a substantial body of knowledge about the occurrence, form and causes of behavioural types has been accumulated over the last two decades, surprisingly little attention has been paid to the ecological, evolutionary and managerial consequences of such differences. The present SAW project aimed to tap into this knowledge gap. By combining theoretical and conceptual research with lab-, mesocosm- and field experiments in different fish models we addressed key research questions at different biological scales ranging from individuals and groups to multi-species communities and socio-ecological systems. The results of this project have been published in 49 peer-reviewed scientific journal articles, including articles in *Nature Communications*, *Trends in Ecology and Evolution*, *Proceedings of the Royal Society*, *Journal of Animal Ecology* and *Fish and Fisheries*. Within the project, two Ph.D theses, seven master and ten bachelor theses have been completed; researchers in our team initiated several follow-up projects resulting in two funded DFG projects, one project funded by the Alexander von Humboldt Stiftung, and two further submitted grant proposals (ERC Starting Grant and NIH Grant, decisions pending).

## Objectives and motivation of the project

Understanding the ecological consequences of biodiversity at all levels of biological organization is of prime social and scientific importance. Biodiversity research has traditionally focussed on the consequences of higher-level diversity, such as species richness, functional group diversity or among-population genetic diversity. More recently, however, behavioural researchers have focussed attention on within-population diversity in behavioural types, that is, behavioural differences between individuals from the same population that are consistent over time and correlated across different contexts (e.g., feeding, antipredator or contest contexts)<sup>1</sup>. An explosion of – typically laboratory-based – research has shown that behavioural types are a widespread phenomenon throughout the animal kingdom<sup>2, 3</sup>. In fish, birds and rodents, for example, some individuals are consistently more aggressive than others, and aggressive individuals are also bolder in response to predators and more active in an unfamiliar environment than less aggressive individuals<sup>2</sup>. Such differences in behavioural traits are often associated with systematic physiological differences<sup>4</sup> in metabolism and stress responses.

While a substantial body of knowledge about the occurrence, form and causes of behavioural types has been accumulated, surprisingly little attention has been paid to the ecological and managerial consequences of such differences. How and when are behavioural types, for example, associated with life history and physiological traits, affect the performance of groups, influence the strength of indirect effects like trophic cascades in multi-species communities, or affect the optimal strategies for sustainable population management? While it has been argued that behavioural types may play an important role for these and related ecological issues<sup>5</sup>, when developing this project, research efforts studying the consequences of behavioural types were in their infancy.

The concluded project took up a pioneering role in this important yet largely overlooked research area. The overarching goal of this project was to generate a holistic and in-depth understanding of the ecological consequences of fish behavioural types and its ramifications for fisheries management. In order to do so, we pursued a highly integrative approach combining theoretical and conceptual research with lab-, mesocosm- and field experiments in different fish models. With this approach we aimed to address basic and applied research questions at different biological scales ranging from individuals and groups to multi-species communities and socio-ecological systems.

In particular, we planned to investigate in five different sub-projects (SPs 1 – 5) the consequences of behavioural types for (i) individual life histories, (ii) group performance, (iii) stability and persistence of populations (iv) aquatic trophic cascades, and (v) recreational fisheries management.

### **SP 1: Consequences for individual life histories**

The goal of SP 1 was to investigate the relation between behavioural types, physiology, and life history. Our main hypothesis was that behavioural types differ systematically in traits associated with life history and physiology, according to the Pace-of-Life syndrome (PoLS) theory. Our goal was to test the prediction that bold and active fish have higher metabolic rate, higher growth rate and earlier maturation than fish with a timid and inactive behavioural type, but have lower life spans. We also aimed to investigate how such trait associations and

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**References:** (1) Sih *et al.* (2004) *TREE* 19:372-378. (2) Sih *et al.* (2004) *Quart Rev Biol* 79:241-277. (3) Bell *et al.* (2009) *Anim Behav* 77:771-783. (4) Biro & Stamps (2010) *TREE* 25:653-659. (5) Wolf & Weissing (2012) *TREE* 27: 452-461.

behavioural types emerge over ontogeny, and on whether laboratory findings also occur under natural conditions.

### **SP 2: Consequences for the performance of groups**

The goal of SP 2 was to investigate the consequences of differences in behavioural types for the performance of groups. Our main hypothesis was that behavioural types differ in their ability to perform different tasks and the ability of groups to perform particular tasks depends not only on the individual abilities but also on the mix of behavioural types present. Our goal was to test three predictions. First, when solitary, individual differences in behavioural types are associated with differences in predator detection tasks and food finding tasks. Second, the performance of groups in the tasks above does not only depend on individual abilities but also on the mix of behavioural types present. In particular, homogenous groups of individually high performers can be outperformed by more diverse groups of individually low performers. Third, the ability of a group to perform a particular task is positively correlated with the ability of that group to perform different but related tasks.

### **SP 3: Consequences for the stability and persistence of populations**

The goal of SP 3 was to investigate the consequences of within-population differences in behavioural types for the stability and persistence of populations. Our main hypothesis was that behavioural types are affected differentially by changing ecological conditions. In variable environments, these differential responses can – when compared to situations without behavioural types – lead to dampened (i.e., less extreme) populations responses, decreasing density fluctuations and extinction risk. Our goal was to test two predictions. First, active types are favoured under high temperatures, less active types under lower ones. Differences in activity levels should thus stabilize populations facing fluctuating temperature regimes. Second, bold types are favoured in low-predation regimes, shy types in high-predation regimes. Differences in boldness should thus stabilize populations facing fluctuating predation pressure.

### **SP 4: Consequences for aquatic trophic cascades**

The goal of SP 4 was to investigate whether and to what extent differences in behavioural types in predator populations affect community interactions in lakes. Our main hypothesis was that the relative frequencies of behavioural types directly correlate with the strength of trophic cascades. Our goal was to test three predictions. First, differences in activity and habitat use between behavioural types in a top predator are associated with differences in diet composition. Second, more active predators have higher encounter frequencies with potential prey, and are more selective with respect to prey species and size. Third, due to their higher selectivity and higher encounter frequencies, active piscivores induce stronger trophic cascades than fish with less active behavioural types.

### **SP 5: Consequences for recreational fisheries management**

The goal of SP 5 was to investigate the implications of fish behavioural type for the success of stocking programs in light of fundamental, behavioural type mediated catch-survival trade-offs and underlying management objectives. We initially expected that behavioural types differ in their vulnerability to fishing gear (active or passive). Our goal was to test the prediction that releasing timid behavioural types increases the sustainability of the stocking event by elevating survival in the wild at the cost of creating low catch-rate fisheries disliked by fishers.

## Development of the conducted work

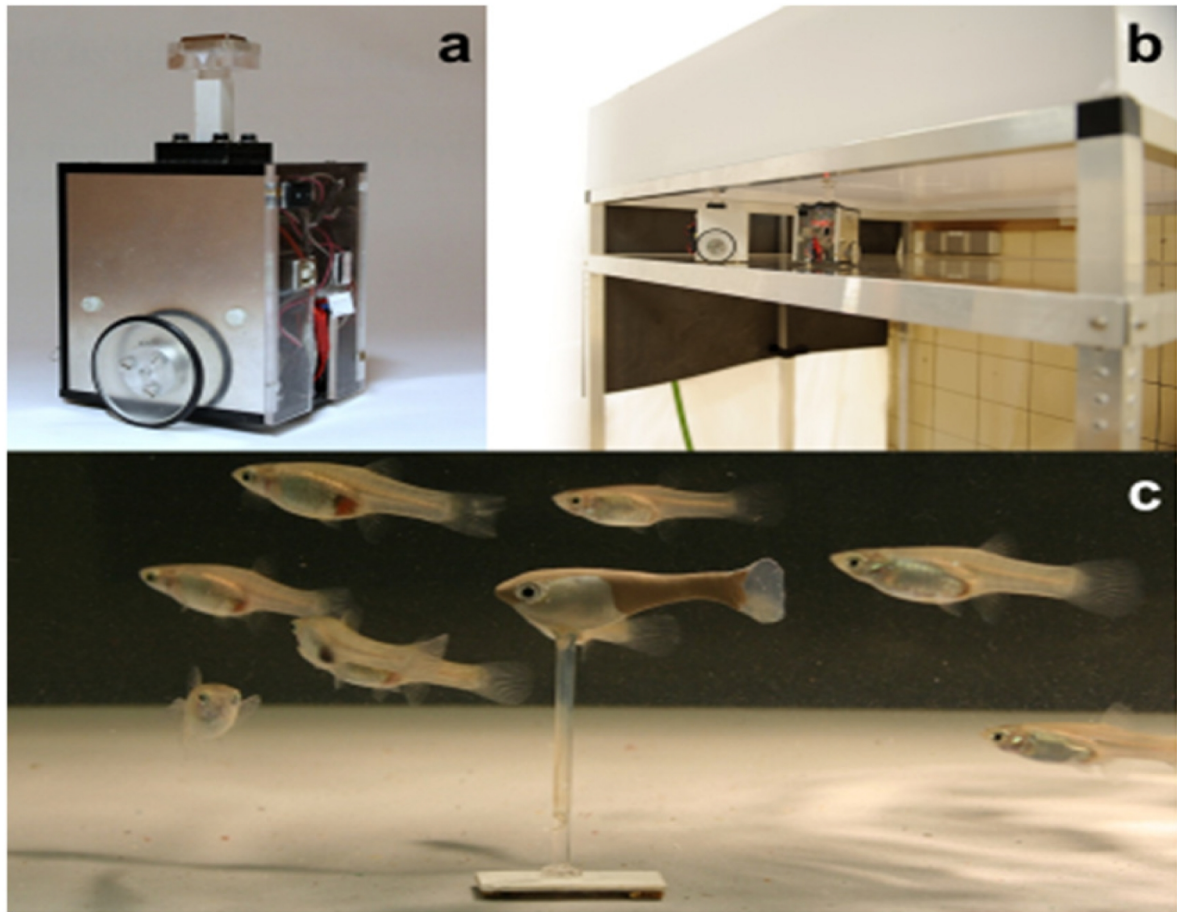
### **SP 1: Consequences for individual life histories**

To test for the associations of behavioural, physiological and life history traits and the development of behavioural types over ontogeny, we quantified individual traits in different life history stages (juveniles, subadults and adults), sometimes even in the same individual. In the laboratory, open-field-, startle-, emergence-, novel-object inspection- and mirror tests were used as standardised behavioural assays to measure activity patterns, boldness-shyness differences, exploration tendency, aggression and sociability. For physiological traits, we focused on metabolism, measured as routine metabolic rate based on oxygen consumption under rest in respirometers. Life histories were quantified in standard life history assays in the laboratory where repeated measures of isolated or marked individuals yield information on growth rates, size- and age-at-maturation, and reproductive success. In the field growth rates were established from hard parts such as scales that form growth rings. Behavioural field data came from an established 3D-acoustic telemetry system in the experimental lake Kleiner Döllnsee (Baktoft *et al.* 2015), based on high-frequency recording of positions of fish carrying passive integrated transponders (PIT-tags).

The experiments conducted partially deviated from the original proposal in the species we used. Instead of using guppies (*Poecilia reticulata*) we conducted laboratory experiments with mosquito fish (*Gambusia holbrooki*) and zebrafish (*Danio rerio*). By doing so, we could use existing populations of mosquito fish in Europe where they are an invasive species. Moreover, we could compare wild populations of mosquito fish outside their native range that differed in the degree of human-caused mortality rate. Zebrafish was added to make use of selection lines of zebrafish existing at IGB which have been harvested over multiple generations in size-selective mortality regimes. This selection of species allowed us to tie behavioural types research to applied questions such as invasion control and impacts on trait variations of human harvesting. The planned field telemetry experiments in Kleiner Döllnsee were done with Northern pike (*Esox Lucius*) and carp (*Cyprinus caprio*), as envisioned, but also with Eurasian perch (*Perca fluviatilis*). The latter species was added to use synergistic effects between the various SPs: Perch as a popular and often targeted species in recreational fishing was also used in SP 5 (see below).

### **SP 2: Consequences for the performance of groups**

We initially tried to establish appropriate tasks to test the hypothesis that the admixture of behavioural types in a group will affect group performances in these tasks. However, we quickly noticed that groups are often inconsistent in their performances, mostly due to mutual, unpredictable interactions among group members. We thus decided to reduce such interactions using two different approaches. In a first approach, we tried to restrict mutual interactions among group members. To do so, we developed a biomimetic robotic fish (**Figure 1**) that is accepted by live fish (guppies in our case, Landgraf *et al.* 2016). With this fascinating and up-to-date method we can now replace live group members by biomimetic robots that can be controlled by the experimenter. In a second approach, we established behavioral assays for a naturally occurring clonal fish, the Amazon molly (*Poecilia formosa*). With this fish species that reproduces gynogenetically we are able to control for genetic differences between individuals and thus investigate the influence of environmental differences on developmental trajectories of individuals. In line with our new set up, we also modified our research questions. In particular, our key focus in this SP was to investigate how social interactions affect the development of individual behavioral differences.



**Figure 1:** The RoboFish system. (a) A wheeled differential-drive robot moves on a transparent platform below the test tank. (b) The robot carries a neodymium magnet directed to the bottom side of the tank. (c, center of image) A 3D-printed fish replica is attached to a magnetic base, which aligns with the robot. Hence the replica can be moved directly by the robot at constant height. (from Landgraf *et al.* 2016).

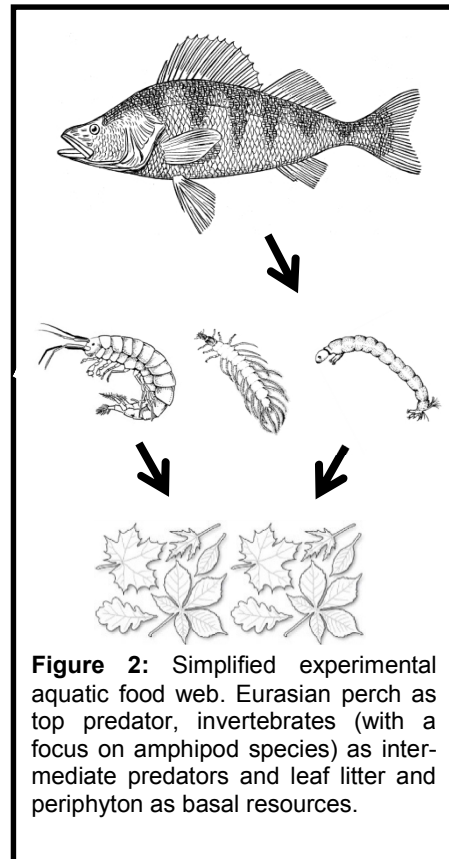
### **SP 3: Consequences for the stability and persistence of fish populations**

This SP was not implemented. Following the organisation of the project, we first wanted to understand the consequences of behavioural types for groups (SP 2), as the population consequences would have built up on such an understanding. However, as outlined above, the implementation of SP 2 proved to be substantially more difficult and challenging than expected, both technically and conceptually. We therefore decided to focus on questions regarding social interactions and group performance and not implement SP 3.

### **SP 4: Consequences for aquatic trophic cascades**

To first aim of SP 3 was to investigate whether behavioural types within predators influenced their diet composition. To test this we took advantage of our acoustic telemetry system at Lake Döllnsee. In this lake we were able to place acoustically-tagged fish (Northern pike) to monitor their behaviour and ultimately determine their behavioural types. Then by taking muscle tissue samples from these fish, we could run stable isotope analyses to determine whether behavioural differences among the fish were correlated with differences in stable isotope signatures indicating differences in individual diets.

To address the other two aims of SP 4 (whether behavioural types in predator influenced encounter rates with prey and whole trophic cascades) was more challenging. To address these questions we needed to develop an experimental food web where we could manipulate the behavioural type composition in the predator population and then measure the resulting responses in the lower levels of the food web. Our goal was to generate a simplified three-level food web (top predator – intermediate predator – basal resource). The difficulty lay in finding a top predator that would not consume the intermediate predator faster than the intermediate predator could consume the basal resource. We experimented with several species including juvenile pike, roach, perch, dragonfly larvae and amphipods. We ultimately were able to generate a food web using Eurasian perch as a top predator, amphipod (and other invertebrates) as intermediate predators and then leaf litter and periphyton as a basal resource (**Figure 2**). However, we also realized that measuring these food webs under laboratory conditions was not feasible in terms of space. Therefore we eventually decided to use the larger outdoor experimental ponds that were available at the IGB. Using this system we were able to explicitly test how the composition of behavioural types in a predator population influenced the whole food web in terms of amphipod (and other invertebrate) abundances, leaf litter decomposition and periphyton growth rates.



### SP 5: Consequences for recreational fisheries management

The original design of SP 5 was to firstly use high-resolution whole-lake telemetry to measure long-term fish behaviour at the whole-lake scale, attempt to capture the individual fish with both active and passive fishing gears, and then relate the behaviour in the lake to the vulnerability to capture. Secondly, the results of the first experiment were to parameterize a mathematical simulation of the relationships among behavioural variation in fish populations, population dynamics and the outcomes of fisheries management objectives. Finally, a proof-of-concept experiment was planned, where fish were to be sorted in a pond environment according to behaviour type and corresponding angling vulnerability. After sorting the fish were to be stocked into multiple large ponds with high, low and mixed vulnerability treatments to test whether the expected differences in vulnerability to multiple fishing gears were indeed present.

Early in SP 5 we realized that the current understanding of the behavioural components of angling vulnerability and selection was much less clear than expected and could not yet inform good models, or the design of fish stocking experiments. Therefore the focus of SP 5 was narrowed and the goal became to understand 1) the behavioural mechanisms of angling vulnerability to passive fishing gears and 2) the ecological and evolutionary consequences of such behavioural-type selective vulnerability. We first explored these questions in a series of review articles. We collected new evidence for the existence of an exploitation induced timidity syndrome in behavioural selectively harvested fish populations, and compiled a list of the likely consequences, and we collaborated on a review of all known scientific information regarding what makes fish vulnerable to hooks. We also conducted two large empirical experiments. In the first field experiment we compared the long-term behaviour of two



benthivorous cyprinids (carp and tench, *Tinca tinca*) at the whole lake scale to vulnerability to experimental angling at baited feeding sites over three months. In the second field experiment we investigated the interaction between fish behaviour and fisher behaviour by tracking adult Eurasian perch in the same lake, while simultaneously tracking experimental anglers of different skill levels. We also attempted to conduct behavioural assays of carp in a pond environment for future sorting purposes; however, the fish purchased for these experiments arrived with a high ecto-parasite load and the high mortality rate reduced the sample size below requirements for proper statistical analysis.

## Presentation of results and their discussion

### SP 1: Consequences for individual life histories

From the various experiments conducted within SP 1 three general findings emerged.

First, and in contrast to a general interpretation of the PoLS theory, physiological, life history and behavioural traits are not always associated with each other. In juvenile zebrafish consistent among-individual differences in activity and risk-taking were found and were negatively correlated with body length but not with routine metabolic rate and body condition (Polverino *et al.* 2016a). A similar result was obtained for Northern pike from field data: we found no relationship between standardized behaviour and any of the measured life-history and physiological state variables, including metabolism, body condition, juvenile growth rate and adult growth rate (Laskowski *et al.* 2016a). In contrast and in line with PoLS predictions, in wild Eurasian perch life-history traits were correlated with behavioural traits such as movements and prey selection. Individual perch with higher reproductive effort were found to switch more frequently between active and inactive modes and show greater reliance on prey from pelagic pathways. Further, individual perch with faster juvenile growth were found to stay active for a longer time during the adult stage (Nakayama *et al.* 2017). Finally we found that repeatable differences in behaviour, metabolic rates, and life-history traits were overall correlated only in a fish population with a slower life history (slow growth etc.), but not in a second population that evolved faster life-history strategies under increased human harvesting (Polverino *et al.* in prep). We also found no effect of existing behavioural types on the size-dependent feeding rates in the Least Killifish (*Heterandria formosa*, Schröder *et al.* 2016). Overall, these results suggest that a general application of the PoLS theory is not possible, and the predicted trait associations may be stage-, context-, and species-specific.

Second, behavioural types can exist even among very young individuals, and the accumulation of experience may drive further divergence (though not necessarily). In juvenile zebrafish strong evidence was found for consistent among-individual differences in activity and risk-taking (Polverino *et al.* 2016a). In contrast, juvenile mosquito fish did not display behavioural types in any of the measured behaviours across context (Polverino *et al.* 2016b) or time (Polverino *et al.* 2016c). However, older mosquito fish and especially their adults now show behavioural types (Polverino *et al.* 2016b, c). This emergence of behavioural types over ontogeny came about through the consolidation of individual behaviour with age: over their life span, a mosquito fish becomes less variable in its behaviour, while among-individual variation was age-independent (Polverino *et al.* 2016c, **Figure 3**). Because intraspecific competition and risk of predation were completely removed and genetic and maternal differences minimized in this study the results strongly suggest that behavioural types might be inevitable and emerge in fish even in absence of extrinsic factors that typically lead to behavioural differentiation (see also SP 2, p. 11, Bierbach *et al.* 2017).

Third, behavioural types also exist in wild populations, and can be quantified with field-based assays. Behaviour of Northern pike within a standardized laboratory assay predicted swimming behaviour in a lake, measured with telemetry (Laswoksi *et al.* 2016 J Fish Biol). A

similar result that allows the transfer of lab-based information to field measurements was found for Threespine sticklebacks (*Gasterosteus aculeatus*, Laskowski *et al.* 2015). Moreover, field-based behavioural types quantified with telemetry can be related to environmental conditions: in Eurasian perch temperature differences over seasons drive the strength of behavioural types which also fluctuates with season (Nakayama *et al.* 2016).

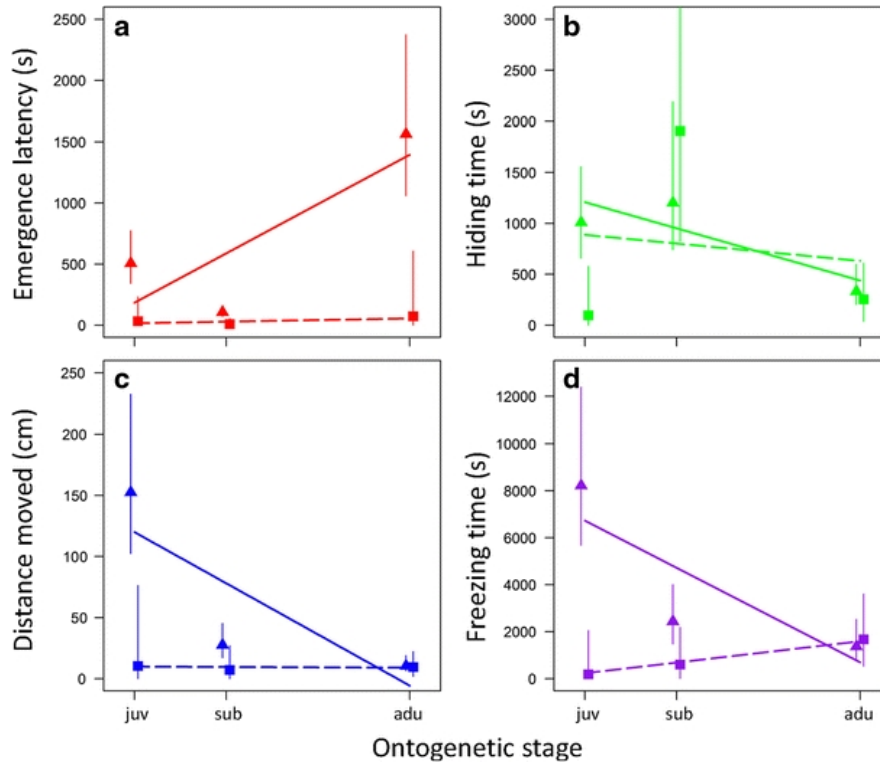


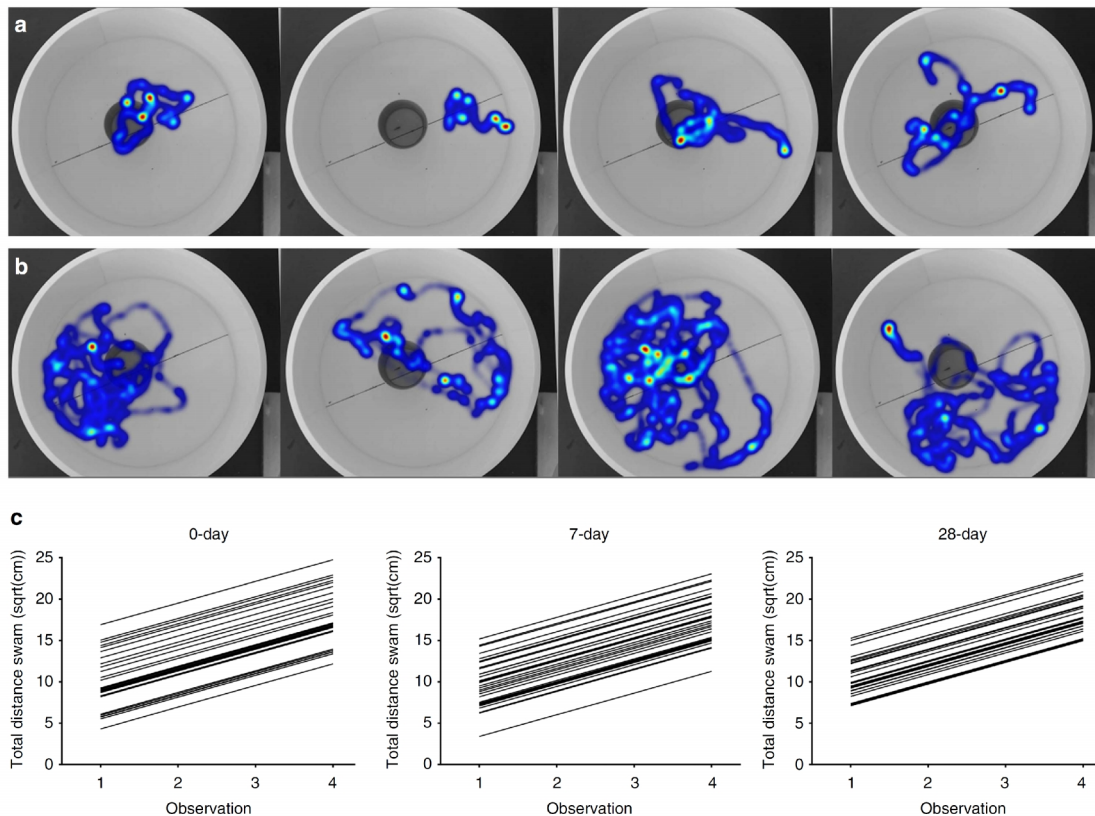
Figure 3: Change in the variance components of behavioral traits within and among individuals across ontogeny, as estimated by linear regressions. Within-individual variance (solid regression lines, medians as triangles) and among-individual variance (dashed regression lines, medians as squares) are shown with respect to (a) “emergence latency”, (b) “hiding time”, (c) “distance moved” and (d) “freezing time”. Medians are represented with respect to juvenile (~5 weeks old), subadult (~10 weeks old), and adult fish (~20 weeks old). Vertical lines represent 95 % credible intervals (from Polverino *et al.* 2016c).

## SP 2: Consequences for the performance of groups

Using our developed RoboFish system which is accepted by live guppies (Landgraf *et al.* 2016), we tested how consistent individual differences in the social responsiveness of live fish affect group performances in a leadership scenario. The robot can either follow its neighbours in the group or, if desired, can assume leadership. Our results show that guppies maintain individual differences in their response towards live companions also when tested with a biomimetic robot. These individual differences are furthermore maintained over a repeated testing with RoboFish though there is some habituation detectable. In addition, guppies differ consistently also in their boldness and general activity with a similar habituation found for the latter. While boldness and activity seem to form a behavioral syndrome with bolder individuals being also more active, social responsiveness towards the RoboFish is not part of this syndrome (Bierbach *et al.* in prep). Further research with RoboFish on social interactions, group behavior and leadership is now funded by DFG (‘Eigene Stelle’ May 2016 – April 2019) that developed from the work in this subproject. This research will not only gain deeper insight into animal group behaviour, but will help to identify general mechanisms that play a role in organizational psychology in humans.

Using our newly established clonal molly model system we found that varying social experiences early in life have profound and long-lasting influences on the performance in a social hierarchy during adulthood (Laskowski *et al.* 2016b). We exposed genetically identical individuals of *Amazon mollies* to repeated winning and/or losing dominance interactions during the first two months of their life. Five months later after sexual maturity, a major life-history transition, individuals that had only winning interactions early in life consistently ranked at the top of the hierarchy. Interestingly, individuals with only losing experience tended to achieve the middle dominance rank, whereas individuals with both winning and losing experiences generally ended up at the bottom of the hierarchy. In addition to demonstrating that early social interactions can have dramatic and long-lasting consequences for adult social behaviour and social structure, these findings also shows that higher cumulative winning experience early in life can counterintuitively give rise to lower social rank later in life.

Although social interactions are thus clearly important in shaping social behaviour, we found in another study with the clonal Amazon molly model system that behavioural types emerge even among genetically identical individuals reared in near identical environmental conditions (Bierbach *et al.* 2017, see **Figure 4**). Moreover, in this study, we also found that raising clonal fish either isolated or in a group of conspecifics led to the very same amount of behavioural variation. These findings are a fundamental challenge to the current paradigm in



**Figure 4:** Individual behaviour in an open-field test over four repeated observations. (a, b) show examples of a less active and a highly active individual, respectively; shown are heat map outputs produced by EthoVision software for each of the four trials. (c) Individual activity levels for the three treatments are shown. Each line represents one individual with the predicted intercept and slope from the models (N = 31 for 0-day and 7-day treatments and N = 32 for 28-day treatment). In all three treatments, we observe substantial among individual differences in behaviour that are repeatable. Neither the level of among-individual variation, nor the amount of total behavioural variation differed between our three treatments (from Bierbach *et al.* 2017).

the behavioural sciences that individual differences are caused by genetic and/or environmental differences between individuals (see also SP 1, p. 9, Polverino *et al.* 2016c).

To explore epigenetic causes of individual differences in clonal fish, we recently applied for an NIH R1 grant in collaboration with Prof. Dr. Wes Warren (University of St. Louis) and Prof. Dr. Manfred Scharl (University of Würzburg). In another follow-up project funded by the Alexander von Humboldt Stiftung (01.02.2018-31.01.2020), Dr. Carolina de Souza-Doran will investigate the co-development of behavioural types and social structure in clonal mollies. Moreover, in a third further follow-up project, Dr. Kate Laskowski (one of our postdocs in this project) submitted an ERC Starting Grant proposal entitled “Using a clonal fish to disentangle the developmental drivers of behavioural individuality” (October 2017).

Next to our experimental work, we developed a series of theoretical-conceptual frameworks addressing key themes investigated in this SP 3. In particular, these frameworks address the development of individuality (Sih *et al.* 2015), the relationship between behavioural types and social structure (Wolf & Krause 2014) and the ecological and evolutionary consequences of social structure (Kurvers *et al.* 2014).

A surprising and completely unplanned outcome of our work in this subproject was the application of our work on fish behaviour to human groups and medical decision making. In this respect, we found that by employing simple aggregation rules (e.g. majority rule) groups of doctors performing diagnostic tasks (e.g. mammography screening) can substantially outperform even the best doctor in that group (Kurvers *et al.* 2015, Wolf *et al.* 2016). Moreover, we found that similarity in diagnostic accuracy is a key condition underlying the superior performance of groups of doctors (Kurvers *et al.* 2016). This exciting line of research is now followed up by Dr. Ralf Kurvers (one of our postdocs in this project) who now holds a research position at the Max Planck Institute for Human Development in Berlin.

### **SP 3: Consequences for the stability and persistence of groups**

Not applicable because the SP was not implemented (see above, p. 7)

### **SP 4: Consequences for aquatic trophic cascades**

In our experiments testing whether individual behavioural co-varied with diet specialization, we took advantage of acoustically-tagged Northern pike in Lake Döllnsee. We used the tracking data from a group of 75 adult pike to generate behavioural profiles of each fish. We found that there was evidence of significant consistent individual variation in both activity (total distance swam), depth and distance from shore. We summarized this behavioural variation in terms of their home range size over the course of 5 months. We then tested whether an individual's behavioural type correlated with its stable isotope signatures, juvenile and adult growth rates, and reproductive success. While analysis of this data is still ongoing, preliminary results indicate that an individual's behavioural type (as measured by home range size) is predicted by its stable isotope signature whereby fish with enriched nitrogen have larger home ranges. Enriched nitrogen signature generally indicates a higher trophic level suggesting that these fish with larger home ranges may be larger, older adults.

The majority of the work in this area was performed using our simplified experimental food web. Here, we performed experiments to test 1) whether perch behavioural type predicted the type of prey the perch consumed in the laboratory and 2) whether the composition of behavioural types in a perch population influenced whole food web dynamics in pond mesocosms. In regards to the first goal, we tested how the behaviour of individual perch and the behaviour of two different species of amphipods (*D. villosus* and *G. roeseli*) influenced the outcome of live predation events between the perch and amphipods. We found strong evidence for perch behavioural types (repeatability of behaviour was > 0.57) and strong differences in average behaviour between the two amphipod species. We also found that one species of amphipod, *D. villosus*, was significantly less likely to be consumed by the perch compared to the other amphipod (*G. roeseli*) in staged predation encounters.

Importantly, perch behavioural type did not influence an individual perch's overall consumption rate or preference for either amphipod species. This suggests that at least in benthic prey such as amphipods, prey behaviour and not predator behaviour is more important in determining the outcome of predation events (Mennen & Laskowski, in review).

We also tested whether the composition of behavioural types in a Eurasian perch population influenced whole food web dynamics using our simplified food web in pond mesocosms. In this experiment we assessed perch behavioural types and then generated three different types of predator groups: groups that contained all bold-active perch ("bold" treatment), groups that contained all shy-inactive perch ("shy" treatment) and groups that contained half bold and half shy perch ("mixed" treatment; N = 6 groups per treatment with 6 perch per group). We placed these small groups of perch into our experimental ponds that had been seeded with local invertebrate communities. We then sampled the invertebrate community abundances and measured leaf litter decomposition and periphyton growth every 2 weeks for 6 weeks. We found that there was a strong effect of the behavioural type treatment on the individual success of the perch. That is, perch with a bold behavioural type gained comparatively more weight when they were in a 'mixed' group as compared to when they were in an all 'bold' group, whereas shy perch did not seem to be affected by the composition of predators (Figure 5). This suggests that the composition of behavioural types in a predator population can have strong effects on the predators themselves, dependent on the predator's own behavioural type. Contrary to our predictions however,

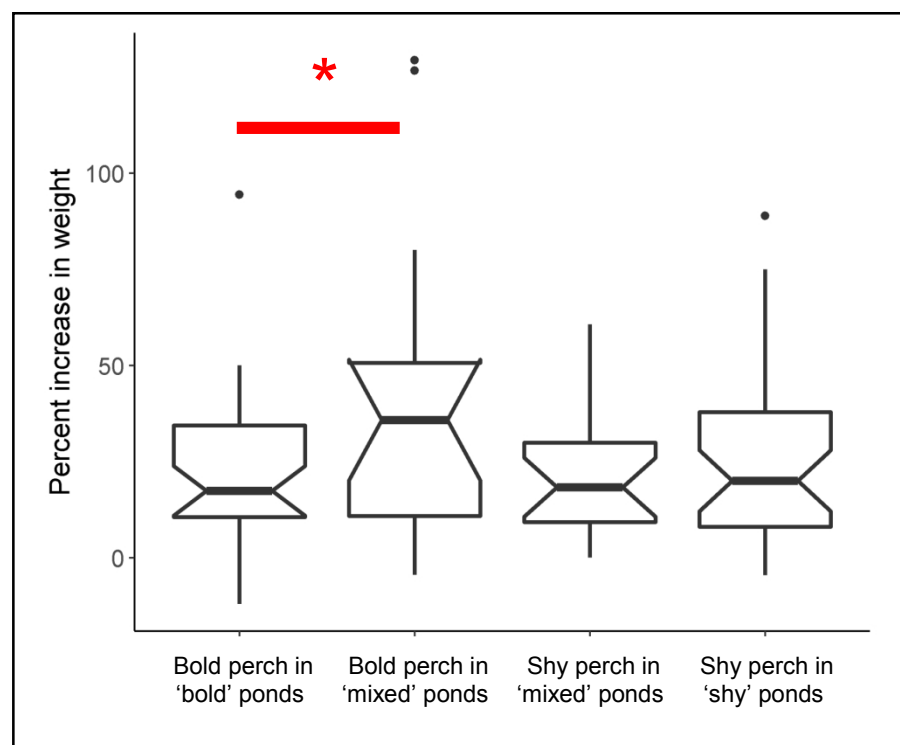


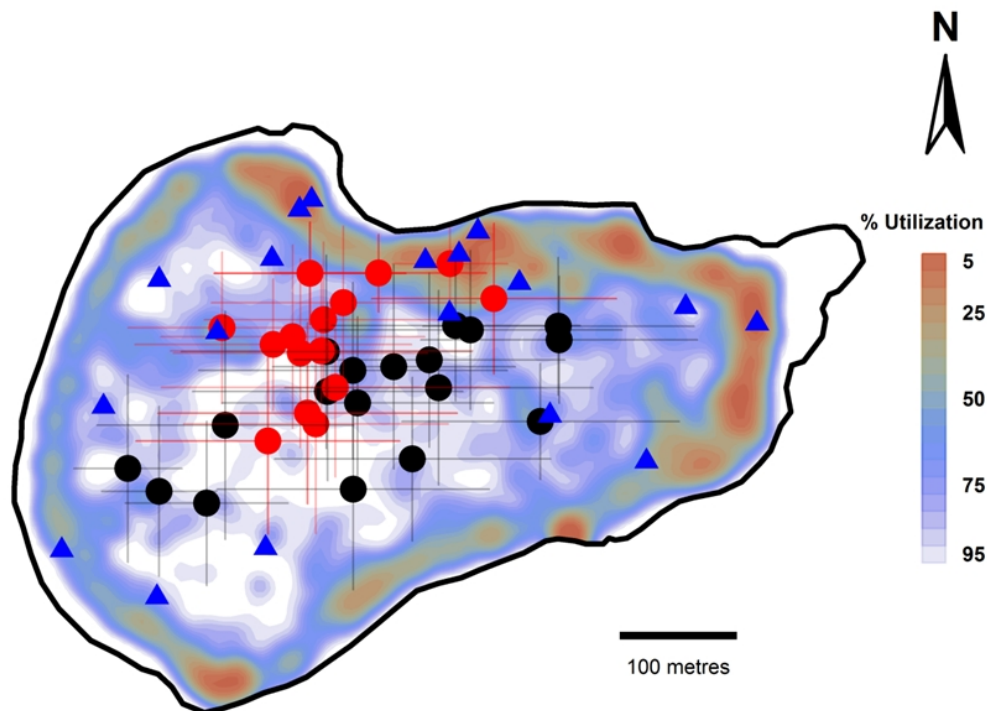
Figure 5: Increase in weight of perch in groups which varied in the composition in behavioural types.

we found that perch behavioural type did not appear to have consistent or strong effects on lower levels of the food web: invertebrate community abundances, leaf litter decomposition rates and periphyton growth rates were all similar across all our treatments. This suggests that the effects of predator behavioural types are likely strong within a trophic level (i.e. the predators themselves) but these effects may attenuate the further down the food chain (Laskowski *et al.*, in prep).

While we initially funded the research in this SP with a two year postdoctoral position, follow-up research is now funded by the DFG ('Eigene Stelle' August 2015 – July 2018) to Dr. Kate Laskowski ("How individual behavioral variation during predator-prey interactions determines invasion success").

## SP 5: Consequences for recreational fisheries management

In our empirical experiments tracking carp, tench and Eurasian perch (Monk & Arlinghaus 2017a, b), we focused on investigating the importance of the encounter component of vulnerability. The high resolution telemetry system is best able to measure activity and movement related behaviours which are thought to modify encounter rate, while the system is less able to measure behaviours like aggression or boldness. In both experiments, we found encounter between the fish and fishing gear was necessary for capture, but was an insufficient predictor of capture, contrary to our predictions. By consequence the activity and movement behaviours we measured, such as distance travelled, activity space size, depth use, time in the open water or distance to the shoreline were also not predictive of capture probability. Some individual carp and tench spent hours at the feeding site on which we were angling without being captured, while other individuals spent comparatively much less time and were captured. Similarly, some individual perch spent little time within casting range of an angler and were captured, while other individuals spent relatively more time within casting range of anglers and were never captured. Therefore we concluded that encounter related behaviours such as activity and space-use were not under selection from angling in these species. Based on our work, fishing-induced selection on encounter-based behaviours in recreational angling for benthivorous fish in the wild appears unlikely. Furthermore, the data cumulatively suggest that fine-scale behaviours after encountering bait may be ultimately decisive for determining vulnerability to angling in benthivorous fish. We have narrowed the possibilities to behaviours acting after encounter and speculate that bait-uptake rates might be important determinants of vulnerability in carp and tench, and habitat specific prey-choice or aggression may be a critical factor in perch (Figure 6).



**Figure 6:** Mean latitude and longitude positions of captured (red points) and never captured (black) acoustically tagged perch and their standard deviations. Blue triangles indicate capture location for these acoustically tagged perch. The background of the lake is the kernel utilization distribution of the fishing locations of all anglers. The white background denotes regions outside the 95% volume contour of the kernel utilization density of the angler's space use. Note that although average positions tend to be near the center of the lake, the perch tend to stay closer to the shoreline (from Monk & Arlinghaus 2017b).

In our review of what makes fish vulnerable to hooks (Lennox *et al.* 2017), we were able to develop a framework for angling vulnerability. We found that angling vulnerability is the outcome of three fundamental components which are modified by factors external and internal to the fish. Importantly, the three fundamental components are the internal state of the fish (e.g., hunger or motivation to bite a lure), the encounter between the fish and the fishing gear, and the suitability of the gear itself. If these three required components are satisfied the fish will be captured. These components are then modified by many factors such as the abiotic and biotic environments, fish movement, morphology, physiology (sensory and metabolic), life-history, cognition and behaviour, and fisheries management restrictions.

In the experiment with perch and perch anglers tracked simultaneously we identified several other noteworthy findings (Monk & Arlinghaus 2017b). First, we saw strong angling-induced habitat selection, where fish spending more time in the north half of the lake showed greater angling vulnerability (**Figure 6**). Unfortunately we lacked the data to explain the mechanisms for this phenomenon. Second, we learned that from an angler's perspective finding more fish is not related to greater angling success, but anglers of higher skill were better able to catch fish they have already found, likely because of better lure control. Moreover, we used a self-classified measure of angling skill based on three simple questions. While such an index of angling skill needs to be validated externally in other fisheries systems, our findings suggest that three questions may be sufficient for a rapid skill assessment during creel surveys and therefore may prove to be a useful tool to assess angling skill. This study has implications for designing protected areas by showcasing that angling could systematically alter the habitat use of exploited populations at whole ecosystem scales, without necessarily changing average swimming activity and home range extension (Monk & Arlinghaus 2017b).

In light of our collective empirical findings and current knowledge of the behavioural components of angling vulnerability, we proposed that fishing with passive gears results in an exploitation induced timidity syndrome, where populations are "consistently more timid when exploited compared to unexploited populations of the same species" (Arlinghaus *et al.* 2016, Arlinghaus *et al.* 2017). We proposed that such increasing population level timidity will have critical ecological and managerial consequences at the social, population, community and fishery levels. To combat the timidity syndrome, we proposed a number of promising management actions to maintain behavioural diversity, such as properly designed protected areas, fish relocation, stocking or size-based harvest regulations.

Collectively, the conceptual and empirical work conducted in SP 5 has filled many gaps identified in our understanding of the behavioural components of fishing vulnerability.

## Statement on patents, economic value and industrial collaborations

Not applicable.

## Contributions from collaboration partners

Not applicable.

## Student qualification projects

### Ph.D. theses

1. Christopher Monk (Feb. 2018). Mining the behavioural reality of fish-fishery interactions to understand vulnerability to hook-and-line fishing. Humboldt Universität zu Berlin.
2. Giovanni Polverino (Dec. 2016). Personality and Pace-of-Life Syndrome in Fishes: New perspectives. Humboldt Universität zu Berlin.

### Master theses

3. Sebastian Theis (2017). Food-dependent development of behavioural types in *Heterandria formosa*. Humboldt Universität zu Berlin.
4. Jasmin Drägestein (2017). Short term effects of artificial light at night (ALAN) on the social behavior of Trinidadian guppies (*Poecilia reticulata*). Humboldt Universität zu Berlin.
5. Juliane Lukas (2017). Behavioral adaptations of a feral guppy population (*Poecilia reticulata* Peters 1859) to temperature gradients in thermally polluted freshwaters. Humboldt Universität zu Berlin
6. Gloria Mennen (2017). The influence of predator behaviour type on invasive prey consumption. Humboldt Universität zu Berlin.
7. Ronja Wenchel (2015). Avoidance of sexual harassment and the role of personality in the guppy (*Poecilia reticulata*). Freie Universität Berlin.
8. Mara Beck (2015). Characterization of the feeding strategies and dietary niche partitioning in a fish community of a small natural lake revealed by stable isotope analyses. Humboldt Universität zu Berlin.
9. Tonio Pieterek (2015). Determinanten der anglerischen Fangbarkeit von Hechten (*Esox lucius*). Humboldt Universität zu Berlin.

### Bachelor theses

10. Philipp Czapla (2017). Verhalten und Aktionsraum von besetzten Hechten (*Esox lucius* L.) in einem natürlichen See: eine telemetrische Untersuchung. Fakultät Umweltingenieurwesen Hochschule Weihenstephan-Triesdorf.
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12. Nadine Muggelberg (2016). Social learning and following behavior towards a biomimetic robot in the Trinidadian guppy (*Poecilia reticulata*). Freie Universität Berlin.
13. Catalina Gliese (2015). Präzygotische reproduktive Isolation zwischen verschiedenen Selektionslinien des Zebraabblings (*Danio rerio*). Humboldt Universität zu Berlin.
14. Johanna Tiefenbacher (2015). Die Rolle der sozialen Umgebung bei der Ontogenie von Perönlichkeitsunterschieden bei klonalen Amazonen-Kärpflingen (*Poecilia formosa*). Freie Universität Berlin.
15. Linda Sartoris (2015). Dominanzhierarchien bei klonalen Amazonen-Käpflingen (*Poecilia formosa*). Freie Universität Berlin.



16. Richard Benthin (2015). Der Einfluss des sozialen Umfelds auf die Entwicklung von interindividuellen Verhaltensunterschieden bei klonalen Amazonen-Kärpflingen (*Poecilia formosa*). Freie Universität Berlin.
17. Tim Evers (2015). Zusammenhang zwischen der individuellen Aktivität und Körperform bei Zebraäbrblingen (*Danio rerio*). Freie Universität Berlin
18. John Brieger (2014). Vergleich des Verhaltens von geangelten und in Stellnetzen gefangenen Barschen (*Perca fluviatilis* L.). Humboldt Universität zu Berlin.
19. Stefan Gehrig (2014). Consequences of animal personality on social partner choice and group performance in the Trinidadian guppy (*Poecilia reticulata*). Freie Universität Berlin.

## List of publications

### 2017

1. R. Arlinghaus, K.L. Laskowski, J. Alós, T. Klefoth, C.T. Monk, S. Nakayama, A. Schröder (2017). Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* 18:360-373.
2. D. Bierbach, K. Laskowski, M. Wolf (2017). Individual differences in behaviour of clonal fish arise despite near-identical rearing conditions. *Nature Communications* 8:15361.
3. R. Lennox, J. Alós, R. Arlinghaus, A. Horodysky, T. Klefoth, C. Monk *et al.* (2017). What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish and Fisheries* 18:986–1010.
4. C.T. Monk, R. Arlinghaus (2017a). Perch (*Perca fluviatilis*) spatial behaviour determines vulnerability independent of angler skill in a whole-lake reality mining experiment. *Canadian Journal of Fisheries and Aquatic Sciences* (online).
5. C.T. Monk, R. Arlinghaus (2017b). Encountering a bait is necessary but insufficient to explain individual variability in vulnerability to angling in two freshwater benthivorous fish in the wild. *PLoS One* 12:1–25.
6. S. Nakayama, T. Rapp, R. Arlinghaus (2017). Fast-low life history is correlated with individual differences in movements and prey selection in an aquatic predator in the wild. *Journal of Animal Ecology* 86:192-201.
7. T. Ruberto, G. Poverino, M. Porfiri (2017). How different is a 3D-printed replica from a conspecific in the eyes of a zebrafish? *Journal of the Experimental Analysis of Behavior* 107:279-293.
8. C. Sommer-Trembo, M. Plath, J. Gismann, C. Helfrich, D. Bierbach (2017). Context-dependent female mate choice maintains variation in male sexual activity. *Royal Society Open Science* 4:170303.

9. J. Alós, M. Palmer, R. Rosselló, R. Arlinghaus (2016). Fast and behavior-selective exploitation of a marine fish targeted by anglers. *Scientific Reports* 6:38093.
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## Statement on data management and access

Data necessary to recapitulate the analyses of any paper published in this project are managed according to the journal-specific requirements, including the presentation of metadata and the data storage in open repositories. Additionally, all data generated by the project are stored on IGB-intern servers and managed according to the IGB data policy statement for environmental field data.

## List of media coverage

Our project received a high coverage in national and international media outlets. In traditional media (print, TV, radio) there were > 100 contributions which covered research results generated by our project or which relied on the expertise and knowledge of the associated researchers. Similar entries related to research and societal impact in science blogs, news pages and fora numbered > 300. Below we give several representative entries for each category, displaying the diversity in topics and coverage achieved.

### **Traditional media (print, TV, radio)**

„Individualität ist nicht zu verhindern“, Pirmasenser Zeitung, 28.05.2017

“Kollektive Intelligenz – Wie große Gruppen Entscheidungen treffen”, Deutschlandradio Kultur, 11.08.2016

„Lieber immer verlieren als manchmal gewinnen“, Bochumer Zeitung, 11.07.2016

“Angeln Verbieten. Freizeitangler und Naturschutz”, 3sat, 07.03.2016

“Roboterfisch aus dem 3D-Drucker”, Südwestdeutscher Rundfunk, 15.10.2015

„Fischerei fördert faule Fische – Forscher untersuchen unterschiedliche Persönlichkeiten unter Wasser und deren Verhalten, das sich etwa durch Angler beeinflussen lässt“, Hamburger Abendblatt, 19.02.2015

„Sind wir nicht alle ein bisschen Hering? – Prof. Jens Krause erforscht das Schwarmverhalten von Fischen und zieht verblüffende Parallelen zu uns Menschen“, Hamburger Morgenpost, 08.02.2015

“Tiere haben Persönlichkeit” Deutschlandfunk, 03.11.2014

„The lives of sociable spiders“, New York Times, 12.05.2014

## Online media (blogs, news pages, fora)

“Same genes, same environment, different personality: Is individuality unavoidable?”. AlphaGalileo. <https://www.alphagalileo.org/ViewItem.aspx?ItemId=175475&CultureCode=en> 17.05.2017

„Gesellschaft unter Wasser - Soziale Netzwerke bei Molly und Muräne“. [www.deutschlandfunk.de](http://www.deutschlandfunk.de), [http://www.deutschlandfunk.de/gesellschaft-unter-wasser-soziale-netzwerke-bei-molly-und-740.de.html?dram:article\\_id=366082](http://www.deutschlandfunk.de/gesellschaft-unter-wasser-soziale-netzwerke-bei-molly-und-740.de.html?dram:article_id=366082). 25.09.2016

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"Der Mensch ist nicht die einzige Art, die schlechter Führung zum Opfer fällt". [MSN Deutschland](http://www.msn.de), 05.02.2016

„Verhaltensforschung mit Guppys“. [www.SWR.de](http://www.swr.de), <https://www.swr.de/blog/diedurchblicker/2015/10/13/fische-mit-persoenlichkeit-verhaltensforschung-mit-guppys/>. 13.10.2015

„Fischereiliche Evolution lässt Fische schrumpfen“, [www.anglerboard.de](http://www.anglerboard.de), <http://www.anglerboard.de/board/showthread.php?t=304820>. 01.07.2015

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