

Individual variation and vulnerability to angling: No apparent behavioral differences among fish captured using different fishing gears

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Abstract

It is well known that fishing is size-selective, but harvest may also inadvertently target certain behavioral types or personalities. Changes in the abundance of behavioral types within a population have implications for fisheries management, including affecting catch rates, individual growth, and food web dynamics. Using streamside behavioral assays, we quantified the repeatability of behaviors in a population of Baikal grayling (*Thymallus baicalensis*) in northern Mongolia, a popular sport fish and important local predator. We assessed whether different angling techniques (i.e., fly or spinning gear) collected different behavioral types and whether variation in behavior was associated with body condition or diet (i.e., using stable isotope analysis). Surprisingly, we found no evidence for consistent individual differences in several behaviors within this population. Furthermore, differences in mean behaviors were not predicted by angling gear, body condition, or carbon and nitrogen isotopic signatures. We suggest that since this is a fished population, the range of behavioral variability in the population may have been reduced through previous behaviorally selective harvest. This might explain both the lack of difference in mean behaviors between fish caught by both gear types and the lack of evidence for consistent individual differences in behavior within the sampled population.

KEYWORDS

animal personality, behavioral type, body condition, fishing vulnerability, selectivity, stable isotope

1 | INTRODUCTION

One of the most immediate reactions an animal can have toward novel conditions is its behavioral response (Sih et al., 2011). Consequently, it is important to identify behavioral responses that allow populations to successfully navigate novel situations in human-altered habitats. An animal's behavior is often moderated by its behavioral type, or consistency in behavioral response across time and/or contexts, also known as its personality or temperament (Sih et al., 2004). While an organism's behavioral type might

influence its own fitness, behavioral type variation in natural populations also affects population dynamics (Sih et al., 2012, Smith & Blumstein, 2008; Wolf & Weissing, 2012). For instance, behavioral variation can influence demographic outcomes via differences in survival and reproductive success between behavioral types (Wolf & Weissing, 2012) or impact habitat carrying capacity when behavioral types utilize habitat differently (Spiegel et al., 2017). Behavioral type has also been shown to affect a forager's diet and even its trophic level in a food web (e.g., Bassar et al., 2010). Naturally occurring behavioral variation could help buffer responses to environmental

change, as different behavioral types might be better suited to respond to different selection pressures brought on by anthropogenic disturbances (Sih et al., 2012; Smith & Blumstein, 2013). Thus, understanding individual behavioral type variation in wild populations facing novel selection pressures is crucial for predicting how best to manage species of concern.

One common anthropogenic disturbance that threatens behavioral type variation in wild populations is harvesting (Diaz Pauli & Sih, 2017; Merrick & Koprowski, 2017; Smith & Blumstein, 2013). Unlike natural predators that might target young or weak prey, harvesting often targets older or larger individuals with preferred phenotypes in a population (reviewed in Merrick & Koprowski, 2017), which could have repercussions for population dynamics and ultimately selection (e.g., Coltman et al., 2003; Darimont et al., 2009; Hutchings & Fraser, 2008). This has become a particular concern in fisheries, especially in overfished populations, since harvesting might be selecting for particular traits such as size, sex, maturity, or behaviors (see reviews Heino et al., 2015; Lennox et al., 2017).

Importantly, fishing techniques, whether active or passive, might be selecting against particular behavioral types (Arlinghaus et al., 2017; Diaz Pauli & Sih, 2017). For example, experimental angling of rainbow trout showed that bolder behaving, faster-growing fish are more often caught than slow-moving, shyer behaving individuals (Biro & Post, 2008). Other studies back up this concern that passive fishing gears (i.e., those in which the capture process requires a specific behavioral response by fish such as biting a hook or entering a trap) might be inadvertently targeting bolder, more aggressive, and/or more active individuals, with overharvesting, potentially removing large swaths of variation from these populations (Cooke et al., 2007; Härkönen et al., 2016; Koeck et al., 2019; Olsen et al., 2012; Wilson et al., 2011). Even small differences in passive fishing techniques can alter targeting of different behavioral types within a population (Härkönen et al., 2016; Wilson et al., 2015). However, variation in experimental results across species and fishing techniques indicate that the link between behavioral type and vulnerability to harvesting is likely species and context-dependent (Diaz Pauli & Sih, 2017; Keiling et al., 2020; Wilson et al., 2011). Vulnerability to capture likely depends on a combination of a fish's internal state, their encounter rate with fishing gear, and that fishing gear's particular characteristics (Lennox et al., 2017). More studies are needed to elucidate these emerging patterns in common fisheries around the world.

These concerns of harvesting bias parallel similar issues of sampling bias in behavioral ecology more generally. Collection, transportation, and acclimation to lab settings all potentially limit natural variation, since each phase represents a potential survival filter (i.e., individuals with certain traits may be more likely to survive each phase). The ultimate concern is that collecting animals from the wild and assaying individuals in controlled laboratory settings will only measure lab stereotypes and not represent true population variation (Archard & Braithwaite, 2010; Biro & Dingemanse, 2009). Furthermore, while some studies have noted that collection techniques bias behavioral variation (e.g., Carter et al., 2012; Garamszegi et al., 2009), other studies have failed to find that bias (e.g., Jolly

et al., 2019; Michelangeli et al., 2016). Trapping bias might be strongest in methods that require animals to respond to novelty, like those of traps or fishing lures, but that might not always be the case (e.g., Jolly et al., 2019). Thus, more studies are needed to elucidate which collection techniques, and in which organisms, biased collection occurs. Furthermore, while there has been a call for more behavioral studies of populations in the wild to address concerns of lab acclimation (Adriaenssens & Johnsson, 2011; Dall & Griffith, 2014), few studies have attempted to experimentally measure behavioral types of fish directly in the field, especially compared with other taxa (but see Brown et al., 2005; Byrnes et al., 2016; Wong et al., 2017 for *in situ* studies).

Thus, a major objective of the following study was to develop an in-field behavioral arena that could be used to repeatedly measure the behavior of wild-caught fish, and elucidate whether differences in fishing techniques might bias the collection of behavioral types. Compared with laboratory studies where the context is often highly artificial or assessments of behavioral variation in field tagging studies where *in situ* movements are quantified without knowledge of the environmental stimuli, our in-field arenas provide a balanced approach by measuring behavior in wild-caught fish in outdoor arenas adjacent to the capture stream. While stream side assays allow limited control over environmental conditions and shorter acclimation times compared with a laboratory setting, they provide substantially more regulation of experience than a field-based experiment. Critically, our in-field arena could easily be broken down and set up, allowing us to systematically measure behavior at multiple remote sites.

To that end, we used our novel in-field setup to measure the behavioral type composition of a population of Baikal grayling (*Thymallus baicalensis*), a common game fish and important drift-feeding predator (Olson et al., 2016) whose population dynamics have important repercussions for their predators and prey. Fish populations in the Selenge River watershed in northern Mongolia are an ideal system to measure baseline individual behavioral type variation in a wild population with limited human impacts, such as flow control and invasive species (Hunt et al., 2016; Kovach et al., 2016). In particular, fish populations are unstocked, naturally reproducing, with a relatively recent (i.e., post-1990s) history of moderate intensity angling (Golden et al., 2019; Jensen et al., 2009). To account for collection bias in our study, we applied two types of angling gear commonly used to target salmonid fishes in rivers, fly, and spinning gear. We collected data on behaviors from behavioral assays that served as estimates of a fish's innate willingness to take risks (sometimes referred to as boldness or exploratory level), which we expect would be critical for responses to novelty. For this study, we define boldness as the relative willingness to move around an unknown space.

We had three main hypotheses going into this study: (1) Individuals caught by spinning gear would be bolder than individuals caught on flies. Due to the nature of its movements across and against the current, a spinning lure creates a greater disturbance and requires fish to actively chase and capture it. Grayling is one

of the dominant prey of adult taimen (*Hucho taimen*) in our study system, and swimming across the river to chase a prey item likely exposes them to considerable predation risk. In contrast, artificial flies mimic a drifting aquatic insect and are typically taken when they pass near a stationary drift-feeding fish. Thus, we expected that the behaviors required to chase a spinning lure are more active and involve more risk-taking than drift feeding (Wilson et al., 2015). Therefore, we predicted that individuals caught with spinning rods would, on average, exhibit greater boldness compared with individuals caught with a fly. (2) Individuals with greater body conditions would be more able to take greater risks for resources (Luttbeg & Sih, 2010). Thus, we predicted a positive relationship between grayling body condition (i.e., approximated by Fulton's K) and measures of fish boldness described above. Alternatively, individuals with the lowest body condition might be more willing to take risks for resources, resulting in a negative relationship between body condition and boldness (Mangel & Clark, 1986; McNamara et al., 1994). (3) Differences in foraging behavior would be reflected in different prey preferences between fish in this population. Thus, using stable isotope analysis to define diet groups, we expected that fish caught by spinner would have a higher trophic level ($\delta^{15}\text{N}$) than fish caught on fly.

2 | METHODS

2.1 | Study system

Fish collection and behavioral assays were performed at two sites within the Selenge River watershed in northern Mongolia during June and July 2018, (1) along the Uur River approximately 10 km above the Eg-Uur confluence (the Uur site) and (2) along the Eg River approximately 10 km above the Eg-Selenge confluence (the Eg site). The two fishing sites are located approximately 251 river kilometers apart. We assayed the behavior of Baikal grayling that were between 151- and 284-mm standard length (mean = 183.7 mm). Size was restricted to those individuals large enough to be held within netted areas of housing and acclimation nets but small enough to cross the barrier within the behavioral assays (detailed below). Baikal grayling in this watershed are generalist feeders consuming a variety of aquatic and terrestrial invertebrates and a small proportion of fish (Olson et al., 2016), such that potential variation in behavior might be reflected in differences within an overall broad diet.

2.2 | Collection and housing

We caught 31 grayling within one km of our Uur assay site and 36 grayling within one km of our Eg assay site (total $N = 67$ individuals, 38 fly and 29 spin caught) using two different angling techniques: fly or spin. The fly fishing technique used a 10–12 mm dry fly (Parachute Adams and Royal Wulff pattern). The spin fishing technique used a Mepps 8th ounce spinner with a single hook. Two



FIGURE 1 Image of both uncovered (left) and covered (right) behavioral arenas in their field setting

experienced anglers caught the majority of fish using a mix of spin and fly techniques; however, some fish were caught by novice members of the team using spin.

After fish were caught via either technique, each individual was brought back to the assay site and housed in an individual netted area (to keep track of individuals while allowing them visual and olfactory cues from conspecifics) within a 244 cm diameter housing pool with 46 cm high walls (Intex). At the Uur site, the housing pool was located 20 m from the river, while at the Eg site, the housing pool was located 13 m from the river. In order to maintain temperature and oxygen close to river levels, the housing pools at each camp were located in the shade, covered with a tarp during the hottest part of the day, and outfitted with aerators. Furthermore, fresh water from the river was added to the housing pool 3–4 times per day at approximately a 50% water change each time. Water was pumped from the river at approximately 18–25 cm depth in the river for both the housing pool and the behavioral arenas. Although offered pellets *ad libitum*, fish in the housing pool preferred consuming terrestrial insects that fell into the water, with 42 out of the 67 individuals containing terrestrial insect remains in their post-mortem gut dissections. Due to signs of disease or injury in eight individuals, behavioral data from only 59 fish were used in our analysis.

2.3 | Behavioral assays

The behavioral arenas consisted of a 244 cm diameter pool (Intex) filled to an approximate depth of 19 cm (uneven natural ground allowed for up to two cm difference in depth between regions of the pool). In order to minimize the influence of another individual's olfactory information and maintain river-like temperature and turbidity, 50% of the water in each arena was changed after each assay. In order to imitate natural conditions, the behavioral arenas were placed within 20 m from the shore of the main stem of the river. Two assay arenas were set up at each site. Above the arena pools, a PVC frame was constructed on which a GoPro Hero camera was mounted

above the center of the arena. Above the PVC frame, white tarp was draped to minimize glare on the camera and limit visual cues from potential aerial predators (Figure 1).

Fish were given a 24 h acclimation period in the housing pool before beginning behavioral trials. To begin behavioral assays at both sites, each fish was removed from the housing pool using a net, placed in a bucket filled with water from the housing pool, and walked 76 m to the behavioral arenas, where they were gently poured into a 30 cm diameter acclimation net on the side of the arena. The acclimation net allowed each individual to receive olfactory and visual cues from the arena before gaining physical access to it entirely. In addition, each arena was bisected by a tarp and PVC barrier, which contained a 10-cm diameter hole in its center, through which each fish could easily move.

The behavioral assays were as follows: After 10 min, the acclimation net was lifted, so that fish were free to move around the bisected arena. Latency to explore or move after receiving access to an arena is a common metric of boldness behavior for many fish species (Brown et al., 2005; Cote et al., 2010). Fish were then allowed to swim around the bisected arena for 10 min post release. During this time, we recorded their latency to first cross the barrier, and the total number of times they crossed the barrier. We categorized bolder fish as those which more quickly cross a barrier into an unknown portion of the arena and cross between the two sides of the arena more times over the course of the trial period.

After 10 min, the barrier was removed and fish were given 10 more minutes to explore the open arena, another common test of animal boldness (Dall & Griffith, 2014). Since the removal of the barrier represented a disturbance, we measured the time each individual spent in the center versus edge of the open arena beginning 5 min after the barrier was removed. A fish was considered along the edge of the arena if it was within one body length of the edge of the pool. We defined bolder fish as those that showed less anti-predator behavior (hugging the edge of the wall) and therefore spent more time moving around the center of the arena.

After each set of behavioral tests, fish were removed from the arenas using a net and transported back to the housing pool in a bucket. All assays were filmed so that behaviors could be scored using Jwatcher software (Blumstein & Daniel, 2007). Each fish experienced the same set of assays three times over the course of three separate days in order to measure repeatability. However, due to camera failure, turbidity after a heavy rainstorm, or unseasonably high water temperatures, we were only able to measure two sets of assays for eight individuals (whereas the other 51 had three repeat measurements of behavior).

2.4 | Dissection and stable isotope collection

After 3 days of behavioral trials, fish were euthanized and dissected to determine sex and remove a 1 x 3 cm tissue sample from the white dorsal musculature for stable isotope analysis. Standard lengths and total weights were recorded. The white muscle tissue was initially

dried in the field using solar radiation and transported back to lab facilities at Rutgers University, where they were stored in a freezer at -80°C . For analysis, samples were dried in an oven for 24 h and then immediately ground with mortar and pestle into a fine powder. Samples were weighed (between 0.85 and 1.17 mg) and packaged in tin capsules. Samples were analyzed at the UC Davis Stable Isotope Facility for ^{13}C and ^{15}N isotopes using a Micro Cube elemental analyzer (Elementar Analysensysteme GmbH) interfaced to an Isoprime VisION IRMS (Elementar UK Ltd). The long-term standard deviation is 0.2 per mil for ^{13}C and 0.3 per mil for ^{15}N (J. Matthews, unpublished data). Since fish white muscle is sufficiently low in lipid content, and the C:N ratios in our samples were less than 3.5 (range 3.47–3.17), it was not necessary to correct carbon values for lipid content (Skinner et al., 2016).

The methods described above were approved by Rutgers University's Institutional Animal Care and Use Committee (Protocol # PROTO999900135).

2.5 | Analysis

We analyzed measured outcome variables (latency to cross a barrier, number of barrier crosses, amount of time in center of arena) using a Bayesian generalized linear mixed modeling framework with the *brms* package (Bürkner, 2017) in R. Latency to cross the barrier and number of barrier crosses were modeled with hurdle-negative binomial distributions (because of zero inflation in these metrics). This mixture model allowed us to incorporate whether an individual performed the behavior (i.e., a Bernoulli distribution in the hurdle), and if they did perform the behavior, the variation in the time or frequency with which that behavior was performed (i.e., a negative binomial distribution). The amount of time in center of arena was modeled using a negative binomial distribution only because this metric did not show zero inflation. In all models, trial order, fishing technique, standard length (centered to a mean of zero and standard deviation of one), and sex were included as fixed effects, with individual identity (ID) and arena included as random effects. All models were built with weakly informative priors and ran for 5000 iterations with 1000 warm-ups. Model diagnostics were checked using the *Shinystan* package (Stan Development Team, 2018). All chains in all models converged properly and showed reasonable effective sample sizes. Non-significant predictors were systematically removed from the original model structure until the WAIC score of the simpler models was higher than a more complex model (i.e., the one with more predictor variables, see Tables S1–S3 in Appendix 1 for details). Temperature was also included as a predictor in simpler models but was not found to be a strong predictor of behavioral outcomes. Since temperature data were only available for 70% of the trials, it could not be used to compare models using WAIC and was not included in final model selection. During 6 trials, individuals crossed underneath the barrier instead of through the hole provided, however, removing those trials did not affect model outcomes, and thus they were included in the reported analysis.

To assess the relationship between body condition and mean behaviors, separate models were constructed for each behavioral outcome using the best-fit models from the previous selection rounds and including Fulton's K (calculated from standard length and wet weight) as a predictor variable (centered to a mean of zero and standard deviation of one). To assess if isotopic signatures were predicted by fishing technique, a multivariate model was constructed with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ as outcome variables (both centered to a mean of zero and standard deviation of one, treated as a Gaussian distribution) with population and fish technique as predictor variables. In addition, post-hoc analysis was conducted to assess whether there were differences in length or body condition between fishing technique or population.

To assess individual variation within our sampled population, we calculated the repeatability (i.e., ICC, variance ratio, or pooling factor, Gelman & Pardoe, 2006) for each behavior using the "performance" package (Lüdecke et al., 2019) in R. Using this method, credible intervals for the estimate of the variance ratio can overlap zero. The negative variance ratio credible intervals can be explained as follows: if most of the model variance is due to within-individual effects and there is little between-individual variation, then the variance of predicted draws will be very similar whether individual-level variation is taken into account or not. In this case, the distributions of predicted variance will be very similar between conditional and unconditional draws. As such, when subtracting one distribution from the other, as is done in calculating the variance decomposition ratio, the difference will be centered to zero, but the tails of the distribution may extend below zero. This is not suggesting that the actual estimate of the variance ratio is below zero, it is simply a byproduct of calculating the difference between two very similar distributions of variance estimates.

Data and scripts used to generate analysis can be found at <https://github.com/ljpollack/Grayling_personality_models>.

3 | RESULTS

Neither trial order, fishing technique, length, nor sex influenced likelihood to cross the barrier, latency to cross barrier, number of barrier crosses, or amount of time spent in center (see Table 1 for posterior parameter estimates for fixed effects in best-fit model). There was one exception to this trend in that there was a negative effect of length on the number of individual barrier crosses (estimate = -0.44, est. error = 0.15, 95% CI = -0.73 to -0.14).

We did not find evidence of repeatability in any of the behaviors measured. That is, the variance ratios based on individual ID calculated from our best-fit models have wide credible intervals that overlap with zero (likelihood to cross a barrier: variance ratio = 0.13, 95% CI = -0.12 to 0.49, latency to cross a barrier: variance ratio = 0.26, 95% CI = -1.04 to 0.927, number of barrier crosses: variance ratio = 0.41, 95% CI = -0.62 to 0.92, amount of time in center of arena: variance ratio = 0.15, 95% CI = -1.07 to 0.72), indicating that individual ID does not explain variation in our posterior estimates (see Figure 2 for behavioral data by individual).

There was no effect of body condition (i.e., Fulton's K) on latency to cross the barrier (estimate = -0.14, est. error = 0.14, 95% CI = -0.40 to 0.14), number of barrier crosses (estimate = -0.14, est. error = 0.14, 95% CI = -0.42 to 0.13), or amount of time spent in center (estimate = 0.17, est. error = 0.13, 95% CI = -0.08 to 0.42). However, there was a positive effect of body condition on likelihood to cross the barrier (i.e., the hurdle portion of the model; estimate = 0.95, est. error = 0.46, 95% CI 0.13 to 1.97). That is,

TABLE 1 Best-fit model structure and posterior estimates

Model structure	Posterior parameter estimates for fixed effects				
	Parameter	Estimate	Est. Error	2.5 CI	97.5 CI
Latency to cross barrier released in arena ~1 + trial + standard length + (1 individual ID) + (1 arena) hurdle ~1 + trial + standard length + (1 individual ID) + (1 arena)	Intercept	4.44	0.43	3.59	5.30
	Trial	-0.02	0.13	-0.27	0.24
	Standard length	0.26	0.16	-0.06	0.60
	Hu intercept	-1.02	0.84	-2.66	0.67
	Hu trial	-0.01	0.29	-0.57	0.57
	Hu standard length	0.07	0.44	-0.78	0.94
Number of crosses ~1 + trial + standard length + (1 individual ID) + (1 arena) hurdle ~1 + trial + standard length + (1 individual ID) + (1 arena)	Intercept	1.58	0.56	0.45	2.68
	Trial	0.13	0.11	-0.09	0.36
	Standard length	-0.44	0.15	-0.73	-0.14
	Hu intercept	-1.04	0.85	-2.73	0.65
	Hu trial	-0.01	0.29	-0.56	0.57
	Hu standard length	0.07	0.44	-0.79	0.97
Amount of time spent center ~1 + trial + fishing technique + (1 individual ID) + (1 arena)	Intercept	4.21	0.37	3.50	4.93
	Trial	-0.19	0.14	-0.47	0.08
	Fishing technique	-0.37	0.24	-0.83	0.09

FIGURE 2 Behavior metrics for all individuals. For each plot, individuals are organized by mean behavioral values for that assay only. Each plot represents the raw data from all behavioral metrics: (a) Latency to cross the barrier in seconds, (b) the number of barrier crosses, and (c) time spent in the arena center in seconds. Error bars indicate the minimum and maximum values measured for each individual

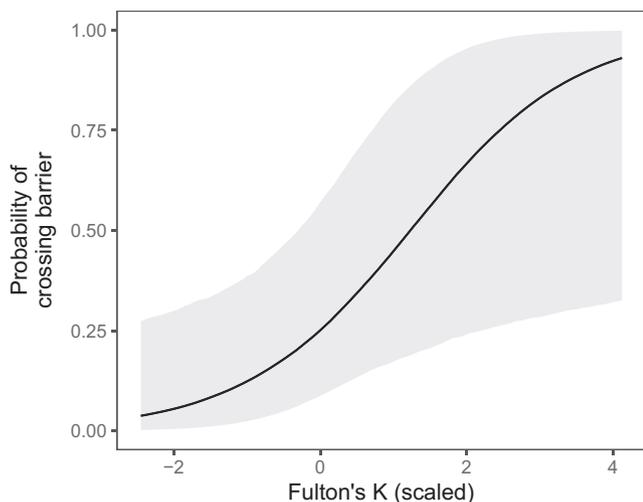
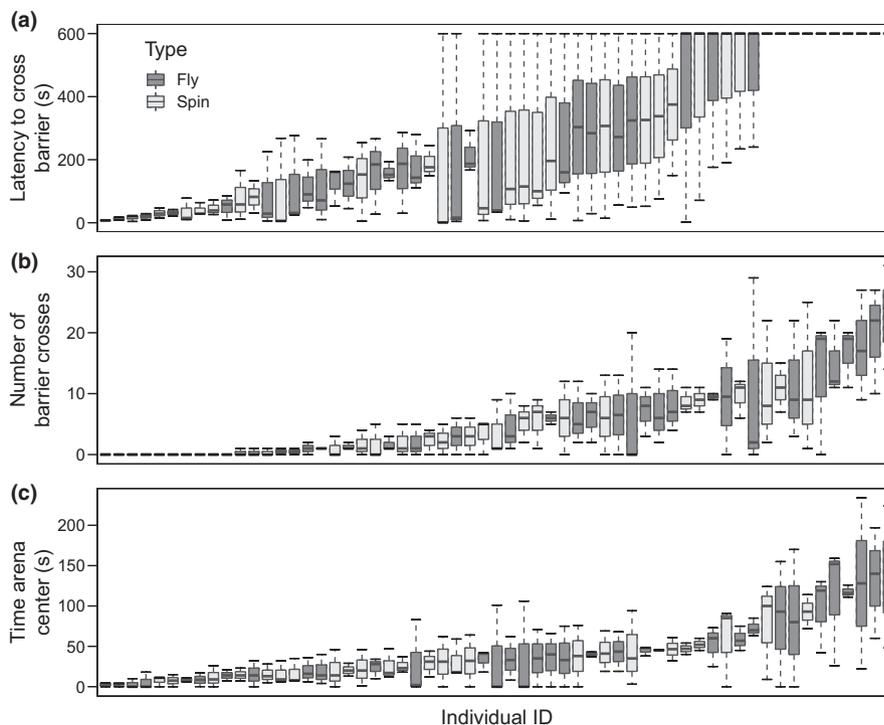


FIGURE 3 Marginal effect of body condition (Fulton's K) on probability of crossing the barrier. The data depicted in Figure 3 is simulated from the hurdle portion of posterior parameter estimates of the mixture model of latency to cross the barrier. The line represents the median effects, while the bands indicate the 95% credible intervals. Values for Fulton's K have been centered to a mean of zero and standard deviation of one before being included in the model

individuals in better body condition (i.e., larger Fulton's K) were more likely to cross the barrier at least once than not cross it at all during the 10-minute trial (Figure 3).

Lastly, there were no differences in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ based on fishing technique (Figure 4). That is, while there was a difference between the Eg and Uur locations in their isotopic signatures ($\delta^{13}\text{C}$: estimate = -0.47, est. error = 0.14, 95% CI = -0.74 to -0.20; $\delta^{15}\text{N}$:

estimate = -1.05, est. error = 0.14, 95% CI = -1.32 to -0.78), there was no difference in isotopic signature based on fishing technique ($\delta^{13}\text{C}$: estimate = -0.18, est. error = 0.14, 95% CI = -0.45 to 0.09; $\delta^{15}\text{N}$: estimate = 0.04, est. error = 0.14, 95% CI = -0.23 to 0.31). There was a residual correlation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (estimate = 0.28, est. error = 0.13, 95% CI = 0.02 to 0.51).

Post-hoc analysis indicated that there were no differences in the length or body condition, of fish caught based on fishing technique (standard length: estimate = 10.83, est. error = 7.72, 95% CI = -4.39 to 26.02; Fulton's K: estimate = 0.07, est. error = 0.03, 95% CI = -0.00 to 0.13). While there was no difference in body condition based on population (estimate = 0.04, est. error = 0.03, 95% CI = -0.03 to 0.10), there was a difference between the Eg and Uur locations in length of fish caught (estimate = 16.74, est. error = 7.75, 95% CI = 1.72 to 31.82).

4 | DISCUSSION

We did not find differences in behavior between individuals caught with fly or spin fishing gear (hypothesis 1). Moreover, we did not find a relationship between most of the behaviors and body condition as approximated by Fulton's K, except for likelihood to cross the barrier (hypothesis 2). That is, fish in better condition were more likely to cross the barrier than not across multiple trials. However, neither mean latency to cross nor the number of times a fish crossed the barrier, both finer scale measures of behavior, were influenced by fish body condition. Assuming that crossing the barrier is a risk-taking behavior, this finding supports the hypothesis that individuals with greater body condition were more willing to take greater risks for resources (Luttbeg & Sih, 2010). Conversely, it could also be that

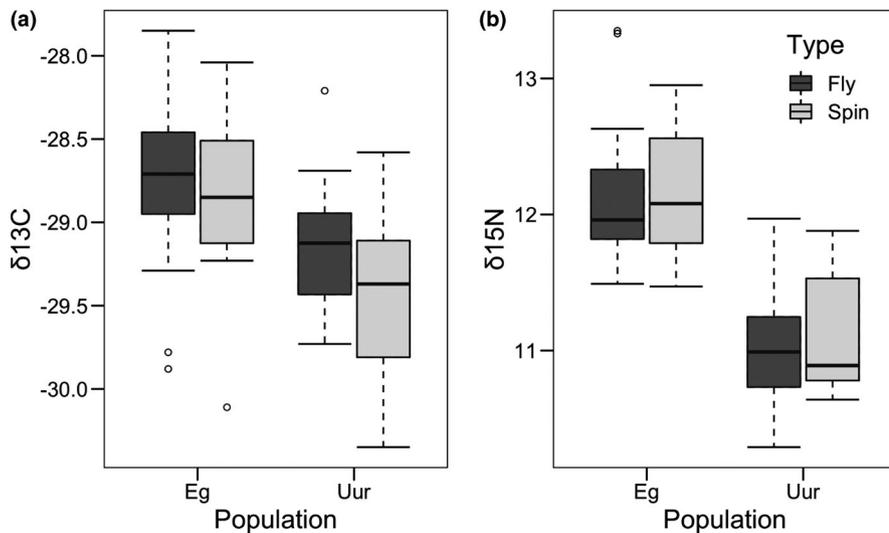


FIGURE 4 Mean isotopic signatures for each population of fly and spin caught fish for either (a) $\delta^{13}\text{C}$ or (b) $\delta^{15}\text{N}$. Error bars indicate one standard error

fish that were more willing to take more risks have better condition in general. Moreover, length did not predict behavioral outcomes except for one, the number of times an individual crossed a barrier; larger individuals tended to cross the barrier fewer times. This trend likely reflected our experimental design more than behavioral differences between individuals of different sizes, since a small opening is less of a constraint for small fish. This is further supported by the other behavioral metrics, which did not find that size was a strong predictor of the other mean behaviors. Lastly, there was no relationship between fishing technique and trophic level as approximated by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic signatures (hypothesis 3).

Critically, we found no evidence supporting our main assumption: that there would be consistent individual differences in behavior within this population of Baikal grayling. The variance ratios based on individual identity calculated from our best-fit models for all behaviors had credible intervals that overlap with zero. This is because the variances conditional or unconditional on group effects were essentially the same if group-level effects were included or not. This suggests that the grouping component (i.e., individual identity) had very little effect on the outcome (i.e., behavior).

Whether this lack of consistent individual differences is due to our experimental design or a true lack of individual variation in behavior within this population is unclear. For one, fish were exposed to a limited set of behavioral assay types, which might not have been able to measure the traits as we predicted (reviewed in Carter et al., 2013). Additional behavioral assays might have allowed us to assess responses across additional ecological contexts, like response to threatening or benign novel objects in addition to novel habitat (e.g., White et al., 2013). A fuller suite of behavioral assays could have provided a more comprehensive assessment of fish boldness in our study. However, other studies have found that certain populations do not demonstrate repeatable individual differences in behavior. For example, a recent comparative study of anemonefishes (*Amphiprion* spp.) showed that while *Amphiprion mccullochi* individuals have high behavioral repeatability, *Amphiprion latezonatus* did not (Wong et al., 2017). The authors hypothesized that this lack of

individual consistency is due to higher variation in the environmental and social conditions for *Amphiprion latezonatus* in their natural environment. If this was the case for the Baikal grayling within this study, high environmental instability in the Selenge River watershed could drive high levels of individual behavioral plasticity. Therefore, the lack of individual consistency we observed could be explained by high within-individual variation within this population, and not necessarily low among-individual variation in our sample.

Another explanation for this finding is that angling in general acts as a strong enough filter for a behavioral type, which could have made it hard to detect differences in the subsequent sample. For example, the steps of an invasion process likely filter out among-individual variation within a population on the invasion front (Chapple et al., 2012). Similarly, if angling was highly selective for bold individuals, there may not have been enough individual variation among individuals captured by both angling techniques to detect significant individual-level behavioral variation (Biro, 2013). In this case, we might assume not that the individuals within our study showed low intra-individual variation, but that we did not catch the individuals within the population that would demonstrate among-individual differences. Thus, without enough variability between behavioral types collected, we were unable to show that there was greater variation between than within individuals. While our sample size was on the smaller side ($N = 67$), it was well within the range of similar studies that have found a relationship between fish behavioral type (i.e., repeatable individual differences) and vulnerability to fishing (e.g., Klefoth et al., 2013; Sbragaglia et al., 2019; Vainikka et al., 2016; Wilson & Godin, 2009). Compared with laboratory-based experiments, our acclimation times were extremely short (i.e., 24 h), which could limit the recovery of fish to handling stress. If this effect was strong enough, it could also mask true differences in behavior between the different groups.

Furthermore, if both angling techniques collected the same behavioral types, it would also explain our finding that there were no differences in mean behaviors between fly and spin caught fish. Similarly, other studies with experimental angling have found a lack

of relationship between boldness and boldness syndromes and capture method (Keiling et al., 2020; Kekäläinen et al., 2014, Vainikka et al., 2016). A recent study of angling vulnerability within experimental ponds with largemouth bass (*Micropterus salmoides*) did not find that boldness behavioral phenotype predicted angling capture (Keiling et al., 2020). However, they found that the angler, not the gear itself, caught fish with different behavioral phenotypes. This indicated that angler skill might have affected behavioral type selection more than gear type, at least with certain techniques. If this was the case in our system, we might have failed to see distinctions in behavior due to gear differences if sampling was biased by the skill of the anglers. This is particularly intriguing in this fishery, where gear types are associated with different demographic groups of anglers (Golden et al., *in press*), in which variation in skill level and gear type might exacerbate differences in fish behavioral types caught between these communities.

In addition to the lack of behavioral patterns due to angling technique, we did not find a relationship between most behaviors and body condition or diet composition. If this finding is connected to sampling bias (i.e., that both angling techniques primarily caught a narrow range of similar behavioral types), then the lack of pattern is not entirely surprising. We might expect that similar behaving individuals would have similar body condition and diet. Moreover, variation in angling vulnerability is not always echoed by variances in diet. For example, even though Klefoth et al. (2013) found differences in boldness between genotypes that demonstrated differences in angling vulnerability, these behavioral differences were not reflected in diet preference studies in the lab. Similarly, Redpath et al. (2009) found no difference in stomach content between largemouth bass that were artificially selected for high and low vulnerability to angling. Thus, even if fish behave differently with respect to their vulnerability to angling, it does not necessarily mean that these same individuals occupy different trophic levels.

By measuring repeated behavior in semi-natural outdoor mesocosm arenas, this study provides further insight into behavioral variation outside a classic laboratory setting. Contrary to prior studies (Härkönen et al., 2016; Wilson et al., 2015), we did not find that angling gear type acts as a selective pressure on fish behavior. Surprisingly, we found no evidence of consistent individual differences within the sampled Baikal grayling population of the Selenge River watershed. This could be due to environmental instability driving high within-individual behavioral plasticity (Wong et al., 2017) or the constraints of sampling and assaying a wild population in a lab-field hybrid design (Archard & Braithwaite, 2010). Most intriguing is that this population is assumed to be relatively undisturbed compared with other fish populations around the world. If we assumed this population is not undergoing fisheries-induced selection, we might conclude that anthropogenic pressures associated with harvesting do not cause the high behavioral plasticity that we observed in this population. In this case, the feature that makes the remote Selenge River watershed ideal for evaluating the behavior of wild populations (i.e., its relative lack of disturbance) might also make it challenging to quantify naturally occurring consistent individual

differences in this population. However, since there are moderate fishing levels in this system, another explanation is that behavioral variation within this population has already been reduced through selective harvest. This would explain both the lack of differences in mean behaviors between fish caught by both gear types and our inability to observe consistent individual differences within the sampled population. Future work using this hybrid field-based assay approach should seek to quantify consistency in behavior across multiple ecologically relevant contexts for a more comprehensive understanding of behavioral repeatability in wild populations.

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