Oceanological and Hydrobiological Studies

International Journal of Oceanography and Hydrobiology

Volume 55, No. 2 June 2026
pages (133-144)

ISSN 1730-413X
eISSN 1897-3191

Exploration in a behaviourally diverse potamodromous fish is not influenced by changes in feeding predictability

by

Dagmara Błońska[1,2]*, Simone Cittadino[2], Ali Serhan Tarkan[1,3], Demetra Andreou[2], J. Robert Britton[2]

DOI: **https://doi.org/10.26881/oahs-2026.1.14**
Category: **Original research papers**
Received: **March 20, 2026**
Accepted: **May 11, 2026**

[1]*University of Lodz, Faculty of Biology and Environmental Protection, Department of Ecology and Vertebrate Zoology, Banacha 12/16, 90-237 Lodz, Poland*
[2]*School of Life and Environmental Sciences, Faculty of Health, Environmental and Medical Sciences, Bournemouth University, Poole, Dorset BH12 5BB, United Kingdom*
[3]*Department of Basic Sciences, Faculty of Fisheries, Muğla Sıtkı Koçman University, 48000, Mentese, Muğla, Türkiye*

Abstract

Recreational angling can involve the regular use of energy-rich, formulated baits. These angling subsidies can represent a significant anthropogenic input into freshwaters and could alter the exploratory and foraging behaviour of individuals. To assess how angling bait exposure influences exploratory behaviour in novel environments, the effect of variable food distribution (random vs predictable distribution) was assessed on the body condition and exploratory behaviour of European barbel *Barbus barbus*, a species of high phenotypic diversity in exploratory behaviour and angling bait consumption. Using hatchery-reared fish, exploratory behaviours were assessed in open arena (OA) experiments following an initial period of fixed food distribution, after which the food distribution pattern was switched to assess their plasticity in exploratory behaviour. Following initial food exposure, all fish showed increased condition, with significantly higher condition in the predictable feeding group. Although exploration time was higher in the random feeding group in both OA experiments, these differences were not significant according to food distribution and fish condition. Although hatchery-reared juvenile fish might differ in their behavioural expression versus wild, adult fish, this study nonetheless suggests that short-term exposure to different food distributions does not alter barbel exploratory behaviour, with individual differences more likely driven by inherent behavioural traits.

Key words: *Barbus barbus,* angling subsidy, open arena experiment, feeding pattern, food distribution

---

* Corresponding author: *dagmara.blonska@biol.uni.lodz.pl*

online at www.oandhs.ug.edu.pl

©2026 Authors, This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs License (http://creativecommons.org/licenses/by-nc-nd/4.0/)

Highlights

- Exploratory behaviour remains stable despite changes in the feeding regime
- Food exposure increased body condition but not exploratory behaviour
- Individual differences outweigh the short-term effects of food distribution

1. Introduction

Fishing for recreation is a popular leisure activity, with approximately 10% of the global population participating (Arlinghaus et al., 2019; Arlinghaus & Cooke, 2009). In Europe, over 50 million people fish, with the activity providing a range of individual benefits, including psychological, health, and nutritional gains, while also generating substantial socio-economic, cultural, and societal values (Cooke et al., 2018). While angling styles differ between the species being targeted, many modern angling methods for freshwater species involve the use of energy-rich, manufactured baits (Britton et al., 2022), with large quantities of these feeds introduced into freshwater ecosystems across Europe (Mehner et al., 2019). These baiting practices represent a significant external nutritional input that may influence fish production and food web dynamics (Mehner et al., 2019).

Angling baits can also act as a major trophic subsidy for fish populations (Arlinghaus & Niesar, 2005; Bašić et al., 2015; Specziár et al., 1997). Although there is often some intra-population variation, angling baits can comprise over 90% of the diet of some species (Britton et al., 2022; Gutmann Roberts et al., 2017). The long-term presence of recreational fishing can influence the fidelity of fish to specific foraging areas by providing a consistent and predictable source of food, with common carp *Cyprinus carpio* Linnaeus, 1758 rapidly learning the position of new feeding areas created by angling bait, which they then exploit repeatedly (Žák, 2021). Supplementary baiting can also increase local fish aggregation (Jurajda et al., 2016). However, considerable uncertainty remains regarding how such anthropogenic subsidies affect the spatial behaviour of different freshwater species and communities, particularly across gradients of angling intensity.

The European barbel *Barbus barbus* (Linnaeus, 1758) (hereafter referred to as ‘barbel’) is a popular target species for recreational anglers due to its relatively large size and fighting qualities (Britton & Pegg, 2011). When exposed to angling bait, some individuals consume these subsidies in high dietary proportions (De Santis et al., 2019; Gutmann Roberts et al., 2017). These individuals are being captured by anglers and have lower levels of chronic stress (Britton et al., 2023). Although this potamodromous and rheophilic species can have large home ranges, including making substantial upstream spawning migrations, approximately 80% of populations are relatively sedentary with limited home ranges (Hunt & Jones, 1974; Lucas & Batley, 1996). These resident barbel have diets heavily dependent on bait subsides whereas vagile individuals have diets that are primarily based on natural prey resources (Błońska et al., 2025).

Behavioural experiments in controlled conditions suggest that these individual differences in movement patterns in wild barbel relate to individual variation along a proactive-reactive behavioural axis, where there are consistent differences in the exploratory, social, and foraging behaviours among individuals (Amat-Trigo et al., 2024). However, there is uncertainty as to whether the high proportion of angling bait in the barbel diet results from fish altering their exploratory behaviours to enable their exploitation of heavily baited areas. It is also unclear whether these behaviours differ when bait availability is random (e.g., requiring more exploration to access) or predictable (e.g., requiring less exploration to access). Accordingly, to understand whether there is a causal relationship between angling bait-related subsidies and the motivation of individuals to explore their environments, the aim here was to evaluate how different baiting regimes influence barbel exploratory behaviour under controlled conditions. We exposed individuals to two distinct feeding regimes, a random distribution (mimicking natural food availability) and a predictable feeding regime (repeated baiting of the same area to simulate recreational angling). Exploratory behaviours of individuals were assessed in two measures: the time spent in an open field arena and their propensity to cross a novel barrier. We hypothesised that fish acclimated to the predictable feeding regime display reduced exploratory behaviour, expressed as reduced activity in the open arena (OA), greater use of shelter, and lower probability of crossing the structural barrier, versus fish exposed to the random distribution. We further hypothesised that reversing the feeding regime results in behavioural plasticity, with exploratory behaviour corresponding to shifts in these behavioural measures in response to the new foraging context. The null hypothesis was that the bait distribution does not affect barbel exploratory behaviour due to fixed phenotypic differences in their behaviours (Amat-Trigo et al., 2024).

2. Materials and methods

2.1. Study animals and experimental setup

The barbel used in this study were of hatchery origin, produced from a single pair of broodstock and raised under uniform conditions, ensuring a consistent background and comparable body sizes (64–88 mm fork length [FL]). In the laboratory, the initial step was tagging each fish with a passive integrated transponder (PIT) tag (7 mm × 1.35 mm; Loligo Systems), measuring fork length (nearest mm), and weighing (to 0.1 g). Tagging was conducted under general anaesthesia (tricaine methanesulfonate; MS222). Previous studies have demonstrated that PIT tagging does not adversely impact survival, growth or swimming performance in barbel (Amat-Trigo et al., 2024; Nagel et al., 2023; Nyqvist et al., 2024). The tagged fish were then acclimated in two groups (*n* = 30 each, *n* = 60 in total) housed in two identical holding tanks (90 L each) for 4 weeks before the experiment. Before fish introduction, tanks were conditioned using a commercial bacterial starter culture to establish biological filtration. Each tank was equipped with continuous aeration (air stones) and artificial shelters (PVC tubes, ~10 cm length, 5 cm diameter) to reduce stress and provide refuge. Water was partially exchanged every second day (approximately 20% of total volume), during which feaces and uneaten food were removed. Water temperature and photoperiod were maintained at 17°C and 10L:14D, respectively, to reflect the natural environment at the time of study. During acclimation, all fish were fed the same diet (pelletised marine fishmeal of 2 mm diameter at ca. 1% of body mass) but under two distinct feeding regimes: predictable feeding (food was delivered at a fixed location in the tank, simulating a regular source of angling bait); and random feeding (food was distributed in a different location each day) (Figs. 1A and 1B). After 4 weeks on their respective diets, fish were individually tested for exploratory behaviour (see *Experimental protocol* section below). Following this first experiment, fish were moved to new holding tanks and assigned the opposite feeding treatment. After an additional 4-week feeding period, the same individuals were re-tested using the same behavioural protocol. Feeding treatments were applied in communal holding tanks, while behavioural testing was conducted on individual fish in separate test aquaria. Between experimental phases, fish were transferred to new holding tanks and assigned the opposite feeding regime, preventing fixed tank effects from being confounded with treatment.

The experimental protocol involved an open field test based on a modified version of the protocol described by Amat-Trigo et al. (2024), previously applied to *B. barbus*. The experiments were carried out in 45 L aquaria, each divided into two sections by an

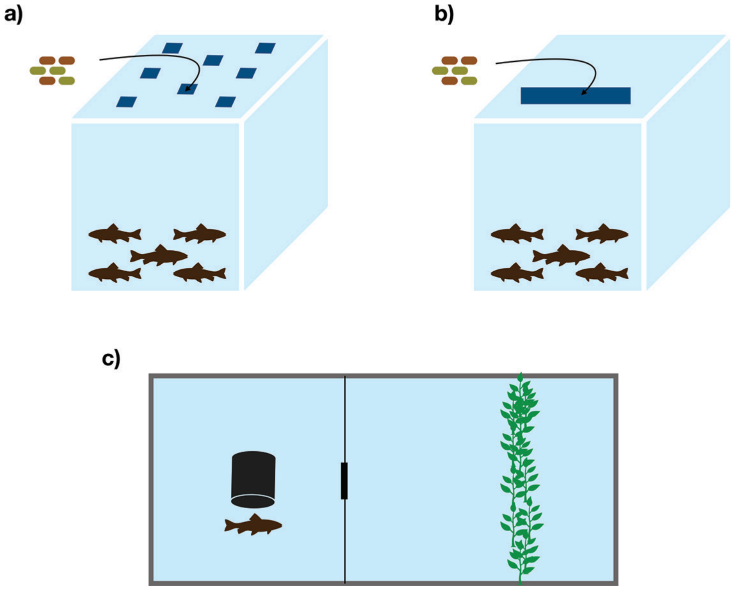

Figure 1

Feeding scheme **(A)** random and **(B)** predictable of European barbel *B. barbus* (Linnaeus, 1758); **(C)** design of experiment arena with an acclimation site equipped with a shelter separated by a sliding door from the OA and artificial plant barrier. OA, open arena.

opaque plexiglass partition featuring a sliding door at the base, which allowed fish to move freely between compartments once opened (Fig. 1C). The first section contained a shelter, consisting of a ~10 cm segment of drainpipe (5 cm radius), matching the shelter type used in the holding tanks. The second section served as the 'open arena' and was further subdivided by a row of artificial plants, which functioned both as a potential refuge and as a low structural barrier (Fig. 1C). All aquaria were surrounded by black screens to minimise external visual stimuli and prevent interaction between individuals in adjacent tanks. Behaviour trials were recorded using crosstour cameras (Action Camera CT7000), positioned above each aquarium. Six fish were tested (individually) simultaneously—three from the random feeding group and three from the predictable group—with a total of 30 replicates per treatment. To standardise motivation levels, fish were fasted for 24 hr prior to testing. All behavioural assays were conducted in February and March 2025. Fish condition was assessed before and after experiments using Fulton's condition factor: $K = 100 \times W \times TL^{-3}$, where: W—body weight (g), TL—total length (cm) (Le Cren, 1951).

2.2. Experimental protocol

Each trial began with a 30-minute acclimation period, during which an individual fish was placed in the shelter section of the aquarium. After acclimation, the sliding door was lifted, allowing the fish access to the OA (Fig. 1C; Amat-Trigo et al., 2024). Behavioural observations commenced immediately after the door was opened (20 min). Two daily testing sessions were conducted: the first between 10:00–10:50, and the second between 11:40–12:30. Between trials, all aquaria underwent complete water exchange to maintain environmental consistency. The following behavioural metrics were recorded from video footage: (i) time spent in or near the shelter, including time aligned closely along shelter exterior, consistent with hiding behaviour, (ii) time inactive in the arena: stationary or resting in the open section, (iii) time active in the arena: any locomotion or exploration in the open area, (iv) crossing of the artificial plant barrier: recorded as a binary variable (yes/no).

2.3. Data analysis

A total of 54 individuals were included in the final analysis (26 initially assigned to the random feeding group and 28 to the predictable group). Six recordings were excluded due to video malfunctions. For each individual, we quantified the duration of each behaviour as a proportion of the total trial time. Exploratory behaviour was defined as active movement of fish in the OA more than 10% of the trial time (over 3 min) and successfully crossing the artificial plant barrier. This 10% activity threshold was based on the distribution of observed activity durations across individuals. Although some individuals entered the arena briefly, these visits were typically short and intermittent, suggesting inspection rather than sustained exploration. In contrast, individuals exceeding the 10% activity threshold consistently engaged with the arena environment and crossed the structural barrier, indicating more extensive exploratory behaviour. To assess individual-level behavioural change between experiments, we applied a categorical scoring system: A value of +1 indicated the emergence of exploratory behaviour in the second trial (i.e. absent in the first, present in the second), −1 indicated a loss of exploratory behaviour (present in the first, absent in the second), and 0 indicated no change (behaviour either present or absent in both trials).

Statistical comparisons of condition factor, shelter use, and activity time between the two experimental phases were performed using the Wilcoxon signed-rank test, following assessment of data normality with the Shapiro–Wilk test. Results are reported as medians with interquartile ranges (IQR). Throughout the manuscript, feeding treatments (random/predictable) refer to the initial feeding regime assigned to each fish. To assess the influence of feeding regime and condition on exploratory behaviour, we used a generalised linear model with a Gaussian distribution and identity link function. The model included the binary variable representing the change in exploratory behaviour as the response variable, with initial feeding pattern (random or predictable) and Fulton's condition factor (*K*) as fixed effects. The response variable represented a directional change index ranging from −1 to +1, centred on zero (no behavioural change). Because this index represents symmetrical deviations around zero rather than an ordered categorical scale, it was analysed using a Gaussian GLM with identity link using the glmmTMB package in R (Brooks et al., 2017). Residual diagnostics and model assumptions (e.g. normality and homoscedasticity) were checked using the DHARMa package (Hartig & Lohse, 2022).

2.4. Ethical statement

The experiment and all regulated procedures were completed under UK Home Office Project Licence PP5256306(P.3) and following ethical approval by the Animal Welfare and Ethical Review Board of Bournemouth University.

3. Results

After 10 weeks (comprised two 4-week feeding phases and two 1-week behavioural experiments: initial feeding regime experiment to changed feeding regime experiment), all fish had increased condition (*K*). Median *K* improved slightly in both groups: individuals initially assigned to random feeding increased from 0.98 (IQR 0.88–1.03) to 0.99 (IQR 0.89–1.04), while those in the predictable feeding group increased from 0.94 (IQR 0.91–0.99) to 1.05 (IQR 1.00–1.09) (Fig. 2). A significant increase in condition was observed only in the predictable feeding group ($V = 69$, $p = 0.002$), with a large effect size (rank-biserial $r = 0.66$, 95% CI [0.35, 0.84]). In contrast, no significant change occurred in the random group ($V = 180$, $p = 0.920$) and the effect size was negligible ($r = -0.03$, 95% CI [−0.43, 0.39]).

Fish spent most of their time in or near the shelter during the trials, with a median of 85% (IQR 11–100) in the first experiment and 90% (IQR 47–100) in the second (Fig. 3A). No significant differences in shelter use were detected within either feeding treatment group across the two experiments (random $V = 88$, $p = 0.54$; predictable: $V = 72$, $p = 0.14$). However, the direction of change differed between groups: shelter use increased in the predictable feeding group (from 68% to 100%) and decreased in the random group (from 93% to 81%).

Fish displayed increased activity in the open field arena during the second experiment, spending a median of 3% of their time (IQR 0%–46%) versus 0% (IQR 0%–15%) in the first trial (Fig. 3B). This pattern likely reflects a treatment effect associated with repeated testing, rather than a feeding treatment effect. The increase was not significant within either feeding group (random: $V = 70.5$, $p = 0.33$; predictable: $V = 65$, $p = 0.60$). The number of individuals classified as exploratory increased in both groups, with a more pronounced change in the fish initially assigned to random feeding (from 9 to 15 individuals out of 26; 40% increase) than in the predictable feeding group (from 8 to 10 individuals out of 28; 20% increase). The results of the Generalized Linear Model (GLM) showed no effect of feeding pattern and condition factor on exploratory behaviour of barbel (Table 1).

4. Discussion

The use of formulated baits in relatively high quantities has been shown to alter the trophic ecology and movements of species including common carp

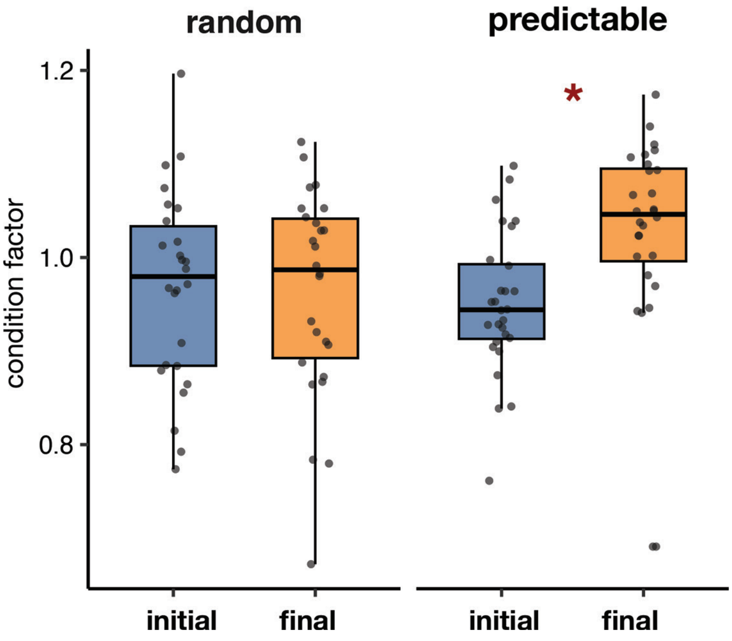

Figure 2

Changes in condition factor between the initial and final status of the tested barbels *B. barbus* (Linnaeus, 1758) ($N = 26$ and $N = 28$ for random and predictable, respectively). Significant difference is marked by an asterisk. Boxplots display the median (bold line), IQR (box edges), and whiskers extending to the most extreme values within 1.5 × IQR. Individual data points are shown as jittered dots. IQR, interquartile range.

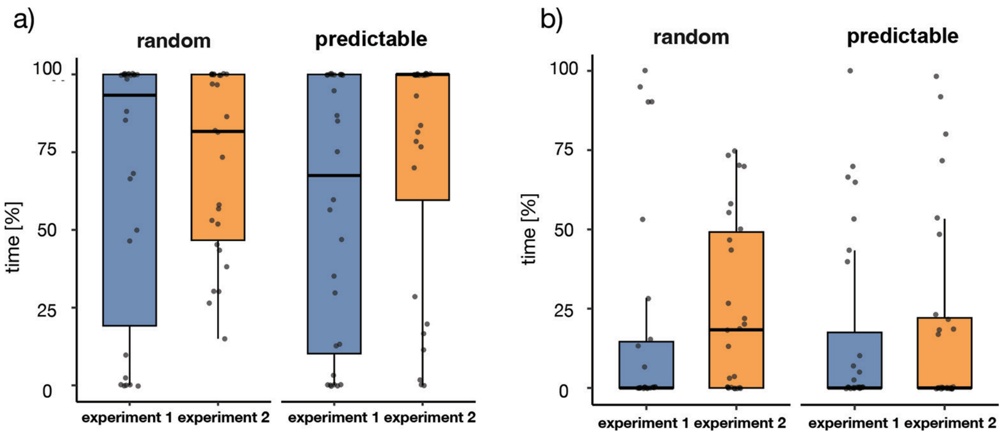

Figure 3

Time spent in/around the shelter (**A**) and time spent active in the experimental arena (**B**) by tested fish in the first and second experiments. Boxplots display the median (bold line), IQR (box edges), and whiskers extending to the most extreme values within 1.5 × IQR. Individual data points are shown as jittered dots. IQR, interquartile range.

Table 1

Summary of Gaussian GLM to model exploratory behaviour of barbel *B. barbus* (Linnaeus, 1758) as a function of initial feeding pattern assigned (random/predictable) and condition factor.

Model parameter	Estimate	SE	*p*
Intercept$_{(random)}$	0.0688	0.066	0.301
Initial pattern$_{(predictable)}$	0.0241	0.100	0.810
Condition	0.2370	0.486	0.612
Initial pattern$_{(predictable)}$: Condition	−1.1245	0.718	0.117

SE, standard error.

(Britton et al., 2022; Žák, 2021). In European barbel, individuals that have limited home ranges usually have higher proportions of angling bait in their diet (Błońska et al., 2025; Gutmann Roberts et al., 2019), raising the question as to whether it is the predictable presence of angling bait in some spatial areas that results in these smaller home ranges or phenotypic differences in the movement ecology of individual barbel is relatively fixed, with barbel with smaller home ranges having more bait in their diet due to greater spatial encounters with anglers. The results here suggested that, in controlled conditions at least, the exploratory behaviour of barbel was not altered by differences in the distribution of food within their tanks, with similar behaviours expressed whether the fish had been exposed to random or predictable distributions. Consequently, we therefore found no evidence that feeding regime altered exploratory behaviour. This may indicate that exploratory tendencies reflect relatively stable individual differences (Amat-Trigo et al., 2024) rather than short-term plastic responses to the feeding manipulation.

Barbel exposed to variable feeding procedures showed an overall improvement in condition, with significant changes in the predictable feeding group. The most frequent behaviour observed was shelter occupation, which constituted over 85% of the experimental time. Exploration activity increased between the treatments as well as the number of exploring individuals, which was more pronounced in the random group. It is also possible that part of the increase in exploratory activity observed during the second trial reflects habituation to the experimental arena, a common response in repeated behavioural assays (Matsunaga & Watanabe, 2010; Rakin et al., 2009). However, our analysis focused on whether the direction of behavioural change differed between feeding regimes and individual condition, allowing us to evaluate treatment-related differences rather than a simple overall trial effect. Although the manipulation represents a simplified proxy, the large effect size observed in the regular treatment indicates a consistent within-individual behavioural shift between phases under controlled conditions. This suggests that spatial predictability can influence behavioural expression at the individual level within this experimental system. However, because feeding treatments were delivered at the tank level and fish were housed together during the feeding phase, these findings should be interpreted as evidence of behavioural responsiveness in this specific experimental context rather than as direct ecological inference. Moreover, the crossover design means that order or habituation effects cannot be fully excluded, and early exposure to one feeding regime may have influenced subsequent responses.

The general improvement in condition was expected, as all fish received the same overall quantity and type of food throughout the experiment. Gutmann Roberts et al. (2017) showed that, under controlled conditions, pelleted fish food enhanced growth rates, particularly when provided in greater amounts. Similarly, under natural conditions, the addition of such a food subsidy has been shown to promote fish growth (De Santis et al., 2019). However, the order of feeding treatments may have influenced the condition gains. Fish fed initially under random conditions had to explore new feeding locations daily, possibly leading to unequal food access during the early days of acclimation. In contrast, fish in the predictable feeding group could rely on a fixed food delivery site, likely reducing competition and facilitating more consistent intake early on. Although feeding regimes were reversed after the first experiment, individuals from the predictable-first group may have retained an early condition advantage. While it remains unclear whether some fish struggled to adjust following the switch, we cannot determine this definitively, as we chose not to sample fish between experiments to minimise handling stress.

The consistent preference for shelter may reflect the species' natural shoaling behaviour (Britton & Pegg, 2011; Hunt & Jones, 1974; Ovidio et al., 2007), as well as the temporary isolation of individuals during experimental trials. Since all behavioural assays were conducted during daylight, a time when barbel are generally more cautious, this may have further reinforced shelter-seeking. The observed divergence in behaviour between treatments could reflect the role of feeding predictability in shaping perceived security. Fish previously exposed to predictable feeding may have developed a strong association between routine and safety. Following the reversal to a random regime, this group may have exhibited increased sheltering as a stress or uncertainty response. Conversely, fish initially subjected to random feeding may have experienced improved confidence and environmental predictability once switched to predictable feeding, leading to reduced shelter use. These patterns suggest that routine may buffer against environmental uncertainty, while unpredictability may initially elicit more cautious behaviour (Gomes & Cardoso, 2020).

Previous work by Amat-Trigo et al. (2024) demonstrated that barbel exhibit a range of behavioural types in controlled conditions, with the majority showing reactive traits. This pattern mirrors observations in the wild, where most individuals display high site fidelity and limited movement (Błońska et al., 2025; Gutmann Roberts et al., 2019; Hunt & Jones, 1974; Peňaz et al., 2002). In contrast, our initial trial identified exploratory behaviour in approximately 30% of individuals (35% and 29% in random and predictable groups, respectively), which rose to nearly 60% in the random-fed group after switching regimes—representing a notable deviation from prior field observations. These differences should be interpreted cautiously. One potential explanation for these discrepancies is the use of hatchery-reared individuals, which ensured a homogeneous developmental background and reduced variability associated with unknown environmental histories. However, hatchery conditions typically differ from natural river environments in terms of habitat complexity and flow variability, which may influence behavioural traits such as activity and exploratory tendencies. However, using wild individuals could have introduced confounding issues associated with the unknown prior experiences of individuals, which would have impaired our ability to test behavioural differences under controlled experimental conditions. Moreover, collecting sufficient numbers of wild stock and of consistent body sizes would have been challenging. Additionally, life-stage effects may also contribute to the observed differences. Juvenile barbel represent a particularly relevant stage for behavioural studies due to their high ecological and behavioural plasticity. During early development, barbel occupy both lentic and lotic habitats, with habitat use shifting ontogenetically as individuals grow (Baras et al., 1995; Copp et al., 1994; Watkins et al., 1997). Smaller individuals are often associated with shallow littoral zones that provide refuge from flow and predation (Copp, 1992; Power, 1987), whereas larger juveniles progressively occupy deeper and faster-flowing habitats (Britton & Pegg, 2011). This transitional stage is therefore characterised by substantial flexibility in habitat use and behaviour, making juveniles particularly suitable for examining responses to environmental variation and feeding regimes. Environmental factors, such as water temperature, flow regime, and habitat structure are also known to influence barbel mobility and behavioural expression (e.g., Błońska et al., 2025; Lucas & Frear, 1997; Panchan et al., 2022).

Neither feeding pattern nor condition factor significantly influenced exploratory behaviour in barbel under controlled conditions. This outcome contradicts our initial hypothesis that a predictable feeding regime—intended to mimic angling bait release—would reduce exploratory tendencies. Given that barbel are known to exploit angling subsidies in the wild, sometimes relying on them for a substantial proportion of their diet (Bašić et al., 2015; Gutmann Roberts et al., 2017; Nolan et al., 2019), we anticipated a corresponding behavioural response under predictable feeding conditions. The absence of a significant effect may suggest that short-term feeding regimes do not strongly influence baseline exploratory behaviour in this species, at least under controlled conditions. Alternatively, it may reflect the overriding influence of intrinsic factors—such as genotype, sex, or developmental stage—on individual movement tendencies (Michelangeli et al., 2022; Niemelä et al., 2022). Further research incorporating longer acclimation periods and/or a broader range of individual-level traits may help to disentangle these influences.

In summary, despite the importance of baited food in fish diet and altered behaviours, the random vs. predictable presence of food did not affect barbel exploratory behaviour under controlled laboratory conditions. High phenotypic variability in behaviour and/or internal factors can play a more primary role in shaping motivational drives compared to external cues. However, this is not the case in all species. Even though common carp displayed individual variability in activity patterns, in general, fish behaviour was strongly affected by predictable feeding (Jurajda et al., 2016; Žák, 2021). These contrasting responses highlight the importance of species-specific traits in shaping behavioural plasticity and underscore the need to consider both intrinsic and extrinsic factors when evaluating the effects of food predictability on fish behaviour. Importantly, these results demonstrate clear behavioural responses under controlled conditions, providing a baseline for understanding how barbel may respond to predictable and unpredictable food sources, while recognising that additional research is required to translate these patterns to natural populations and angling contexts.

Acknowledgement

D. Błońska was supported by a Marie Curie Individual Fellowship HORIZON-MSCA-2022-PF-01 (project 101105250 – PROSPER) within the European Union's Horizon Europe 2022 research and innovation programme, funded by UKRI.

Data availability statement

Data used in the current study are available in the Supplementary Materials (Table S1).

Disclosure statement

The authors report there are no competing interests to declare.

References

Amat-Trigo, F., Andreou, D., Gillingham, P. K., & Britton, J. R. (2024). Individual phenotypic variability in the behaviour of an aggregative riverine fish is structured along a reactive-proactive axis. *Plos One, 19*(11), Article e0312187. https://doi.org/10.1371/journal.pone.0312187

Arlinghaus, R., Abbott, J. K., Fenichel, E. P., Carpenter, S. R., Hunt, L. M., Alós, J., Klefoth, T., Cooke, S. J., Hilborn, R., Jensen, O. P., Wilberg, M. J., Post, J. R., & Manfredo, M. J. (2019). Governing the recreational dimension of global fisheries. *Proceedings of the National Academy of Sciences, 116*(12), 5209–5213. https://doi.org/10.1073/pnas.1902796116

Arlinghaus, R., & Cooke, S. J. (2009). *Recreational fisheries: Socioeconomic importance, conservation issues and management challenges. Recreational hunting, conservation and rural livelihoods: Science and practice* (pp. 39–58). Wiley-Blackwell.

Arlinghaus, R., & Niesar, M. (2005). Nutrient digestibility of angling baits for carp, *Cyprinus carpio*, with implications for groundbait formulation and eutrophication control. *Fisheries Management and Ecology, 12*(2), 91–97. https://doi.org/10.1111/j.1365-2400.2004.00425.x

Baras, E., Nindaba, J., & Philippart, J. C. (1995). Microhabitat used in a 0+ rheophilous cyprinid assemblage: Quantitative assessment of community structure and fish density. *Bulletin Français de la Pêche et de la Pisciculture, 33*(7–339), 241–247. https://doi.org/10.1051/kmae:1995027

Bašić, T., Britton, J. R., Jackson, M. C., Reading, P., & Grey, J. (2015). Angling baits and invasive crayfish as important trophic subsidies for a large cyprinid fish. *Aquatic Sciences, 77*, 153–160. https://doi.org/10.1007/s00027-014-0370-7

Błońska, D., Tarkan, A. S., Andreou, D., Bolland, J. D., Davies, P., Dodd, J. R., Gillingham, P., Roberts, C. G., Amat-Trigo, F., Aksu, S., Hindes, A., Palder, O. J., Yeldham, M., & Britton, J. R. (2025). Restoration of river connectivity enables long-distance spawning migrations in a potamodromous fish. *Journal of Environmental Management, 377*, Article 124646. https://doi.org/10.1016/j.jenvman.2025.124646

Britton, J. R., Andreou, D., Lopez-Bejar, M., & Carbajal, A. (2023). Relationships of scale cortisol content suggest stress resilience in freshwater fish vulnerable to catch-and-release angling in recreational fisheries. *Fisheries Research, 266*, Article 106776. https://doi.org/10.1016/j.fishres.2023.106776

Britton, J. R., Cucherousset, J., & Dominguez Almela, V. (2022). Novel trophic subsidies from recreational angling transform the trophic ecology of freshwater fishes.

Journal of Applied Ecology, 59(9), 2373–2385. https://doi.org/10.1111/1365-2664.14237

Britton, J. R., & Pegg, J. (2011). Ecology of European Barbel *Barbus barbus*: Implications for river, fishery, and conservation management. *Reviews in Fisheries Science, 19*(4), 321–330. https://doi.org/10.1080/10641262.2011.599886

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal, 9/2* 378–400. https://doi.org/10.32614/RJ-2017-066

Cooke, S. J., Twardek, W. M., Lennox, R. J., Zolderdo, A. J., Bower, S. D., Gutowsky, L. F. G., Danylchuk, A. J., Arlinghaus, R., & Beard, D. (2018). The nexus of fun and nutrition: Recreational fishing is also about food. *Fish and Fisheries, 19*(2), 201–224. https://doi.org/10.1111/faf.12246

Copp, G. H. (1992). Comparative microhabitat use of cyprinid larvae and juveniles in a lotic floodplain channel. *Environmental Biology of Fishes, 33*, 181–193. https://doi.org/10.1007/BF00002563

Copp, G. H., Guti, G., Rovny, B., & Černý, J. (1994). Hierarchical analysis of habitat use by 0+ juvenile fish in the Hungarian/Slovak flood plain of the River Danube. *Environmental Biology of Fishes, 40*, 329–348. https://doi.org/10.1007/BF00005279

De Santis, V., Gutmann Roberts, C., & Britton, J. R. (2019). Influences of angler subsidies on the trophic ecology of European barbel *Barbus barbus*. *Fisheries Research, 214*, 35–44. https://doi.org/10.1016/j.fishres.2019.01.028

Gomes, A. C. R., & Cardoso, G. C. (2020). The lag-time constraint for behavioural plasticity. *Proceedings of the Royal Society B: Biological Sciences*, *287* (1926). https://doi.org/10.1098/rspb.2020.052

Gutmann Roberts, C., Bašić, T., Amat Trigo, F., & Britton, J. R. (2017). Trophic consequences for riverine cyprinid fishes of angler subsidies based on marine-derived nutrients. *Freshwater Biology, 62*(5), 894–905. https://doi.org/10.1111/fwb.12910

Gutmann Roberts, C., Hindes, A. M., & Britton, J. R. (2019). Factors influencing individual movements and behaviours of invasive European barbel *Barbus barbus* in a regulated river. *Hydrobiologia, 830*, 213–228. https://doi.org/10.1007/s10750-018-3864-9

Hartig, F., & Lohse, L. (2022). *DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models* (p. 2022). Comprehensive R Archive Network (CRAN).

Hunt, P. C., & Jones, J. W. (1974). A population study of *Barbus barbus* (L.) in the River Severn, England. *Journal of Fish Biology, 6*(3), 255–267. https://doi.org/10.1111/j.1095-8649.1974.tb04543.x

Jurajda, P., Adámek, Z., Roche, K., Mrkvová, M., Štarhová, D., Prášek, V., & Zukal, J. (2016). Carp feeding activity and habitat utilisation in relation to supplementary feeding in a semi-intensive aquaculture pond. *Aquaculture International, 24*, 1627–1640. https://doi.org/10.1007/s10499-016-0061-6

Le Cren, E. D. (1951). The length-weight relationship and seasonal cycle in gonad and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology, 20*(2), 201–219. https://doi.org/10.2307/1540

Lucas, M. C., & Batley, E. (1996). Seasonal movements and behaviour of adult barbel *Barbus barbus*, a riverine cyprinid fish: Implications for river management. *Journal of Applied Ecology, 33*(6), 1345–1358. https://doi.org/10.2307/2404775

Lucas, M. C., & Frear, P. A. (1997). Effects of a flow-gauging weir on the migratory behaviour of adult barbel, a riverine cyprinid. *Journal of Fish Biology, 50*(2), 382–396. https://doi.org/10.1111/j.1095-8649.1997.tb01366.x

Matsunaga, W., & Watanabe, E. (2010). Habituation of medaka (*Oryzias latipes*) demonstrated by open-field testing. *Behavioural Processes, 85*(2), 142–150. https://doi.org/10.1016/j.beproc.2010.06.019

Mehner, T., Rapp, T., Monk, C. T., Beck, M. E., Trudeau, A., Kiljunen, M., Hilt, S., & Arlinghaus, R. (2019). Feeding aquatic ecosystems: Whole-lake experimental addition of angler's ground bait strongly affects omnivorous fish despite low contribution to lake carbon budget. *Ecosystems, 22*, 346–362. https://doi.org/10.1007/s10021-018-0273-x

Michelangeli, M., Payne, E., Spiegel, O., Sinn, D. L., Leu, S. T., Gardner, M. G., & Sih, A. (2022). Personality, spatiotemporal ecological variation and resident/explorer movement syndromes in the sleepy lizard. *Journal of Animal Ecology, 91*(1), 210–223. https://doi.org/10.1111/1365-2656.13616

Nagel, C., Droll, J., Kroemer, K., Pander, J., & Geist, J. (2023). Testing the effects of passive integrated transponder (PIT) tags on survival, growth, and tag retention of common nase (*Chondrostoma nasus* L.) and European barbel (*Barbus barbus* L.). *Animal Biotelemetry, 11*, 33. https://doi.org/10.1186/s40317-023-00344-z

Niemelä, P. T., Klemme, I., Karvonen, A., Hyvärinen, P., Debes, P. V., Erkinaro, J., Sinclair-Waters, M., Pritchard, V. L., Härkönen, L. S., & Primmer, C. R. (2022). Life-history genotype explains variation in migration activity in Atlantic salmon (*Salmo salar*). *Proceedings of the Royal Society B: Biological Sciences*, 289(1978). https://doi.org/10.1098/rspb.2022.0851

Nolan, E. T., Gutmann Roberts, C., & Britton, J. R. (2019). Predicting the contributions of novel marine prey resources from angling and anadromy to the diet of a freshwater apex predator. *Freshwater Biology, 64*(8), 1542–1554. https://doi.org/10.1111/fwb.13326

Nyqvist, D., Schiavon, A., Candiotto, A., Tarena, F., & Comoglio, C. (2024). Survival and swimming performance in small-sized South European Cypriniformes tagged with passive integrated transponders. *Journal of Ecohydraulics, 9*(2), 248–258. https://doi.org/10.1080/24705357.2024.2306419

Ovidio, M., Parkinson, D., Philippart, J.-C., & Baras, E. (2007). Multiyear homing and fidelity to residence areas by individual barbel (*Barbus barbus*). *Belgian Journal of Zoology, 137*, 183–190.

Panchan, R., Pinter, K., Schmutz, S., & Unfer, G. (2022). Seasonal migration and habitat use of adult barbel (*Barbus barbus*) and nase (*Chondrostoma nasus*) along a river stretch of the Austrian Danube River. *Environmental Biology of Fishes, 105*, 1601–1616. https://doi.org/10.1007/s10641-022-01352-3

Peňaz, M., Barus, V., Prokes, M., & Homolka, M. (2002). Movements of barbel, *Barbus barbus* (Pisces: Cyprinidae). *Folia Zoologica (Czech Republic), 51*, 55–66.

Power, M. E. (1987). Predation: Direct and indirect impacts on aquatic communities. In W. C. Kerfoot & A. Sih (Eds.), *Predator avoidance by grazing fishes in temperate and tropical streams: Importance of stream depth and prey size* (pp. 333–351). University Press of New England.

Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., Coppola, G., Geyer, M. A., Glanzman, D. L., Marsland, S., McSweeney, F. K., Wilson, D. A., Wu, C. F., & Thompson, R. F. (2009). Habituation revisited: An updated and revised description of the behavioral characteristics of habituation. *Neurobiology of Learning and Memory, 92*(2), 135–138. https://doi.org/10.1016/j.nlm.2008.09.012

Specziár, A., Tölg, L., & Bíró, P. (1997). Feeding strategy and growth of cyprinids in the littoral zone of Lake Balaton. *Journal of Fish Biology, 51*(6), 1109–1124. https://doi.org/10.1111/j.1095-8649.1997.tb01130.x

Watkins, M. S., Doherty, S., & Copp, G. H. (1997). Microhabitat use by 0+ and older fishes in a small English chalk stream. *Journal of Fish Biology, 50*(5), 1010–1024. https://doi.org/10.1111/j.1095-8649.1997.tb01626.x

Žák, J. (2021). Diel pattern in common carp landings from angling competitions corresponds to their assumed foraging activity. *Fisheries Research, 243*, Article 106086. https://doi.org/10.1016/j.fishres.2021.106086

Supplementary Materials

Table S1

Results of the experiments conducted on barbel *B. barbus* under two feeding patterns: random and predictable.

Fish ID	Initial pattern	K1	K2	Shelter1	Shelter2	Activity1	Activity2	Exploratory
17413	random	1.002	0.86719	0.00	0.30	1.00	0.70	0.00
17478	random	1.0986	0.98019	0.50	1.00	0.00	0.00	0.00
17473	random	0.9674	1.05245	1.00	1.00	0.00	0.00	0.00
17454	random	0.9714	0.7839	0.03	0.73	0.00	0.27	1.00
17416	random	0.9956	0.93184	0.00	0.82	0.00	0.18	1.00
17437	random	1.0527	1.03684	1.00	0.15	0.00	0.75	1.00
17410	random	1.1965	0.98251	1.00	0.58	0.00	0.22	1.00
17470	random	1.108	1.02906	0.00	0.38	0.95	0.58	0.00
17461	random	0.9619	0.90999	1.00	0.30	0.00	0.70	1.00
17434	random	0.7737	0.92027	1.00	1.00	0.00	0.00	0.00
17485	random	1.0567	0.77982	0.10	0.45	0.90	0.55	0.00
17472	random	0.8645	0.99125	1.00	1.00	0.00	0.00	0.00
17453	random	1.0389	1.0178	0.00	0.87	0.00	0.13	1.00
17486	random	1.0169	0.87238	0.85	0.82	0.15	0.18	0.00
17419	random	0.9649	1.02874	1.00	0.97	0.00	0.03	0.00
17463	random	1.0128	1.12356	1.00	0.57	0.00	0.43	1.00
17475	random	0.9087	1.01172	1.00	1.00	0.00	0.00	0.00
17443	random	0.885	1.05266	1.00	1.00	0.00	0.00	0.00
17433	random	0.8793	1.10712	1.00	1.00	0.00	0.00	0.00
17488	random	1.0742	0.88778	0.00	0.53	0.90	0.47	0.00
17487	random	0.7924	0.86431	0.98	0.97	0.00	0.03	0.00
17411	random	0.9878	1.0776	0.68	0.27	0.13	0.73	0.00
17496	random	0.8841	0.90666	1.00	0.52	0.00	0.20	1.00
17422	random	0.9975	1.07495	0.47	1.00	0.53	0.00	−1.00
17495	random	0.8148	0.67221	0.67	0.43	0.28	0.50	0.00
17498	random	0.8555	1.04309	0.88	1.00	0.07	0.00	−1.00
30848	predictable	0.9645	1.09274	1.00	0.12	0.00	0.53	1.00
30867	predictable	0.8408	1.00105	1.00	1.00	0.00	0.00	0.00
30882	predictable	1.0617	1.06685	0.75	1.00	0.00	0.00	0.00
30811	predictable	0.9141	1.04934	0.00	1.00	0.00	0.00	0.00
30895	predictable	1.0389	1.11474	1.00	1.00	0.00	0.00	0.00
30886	predictable	0.964	0.69098	0.00	0.77	0.00	0.23	1.00
30849	predictable	1.0391	0.98105	0.95	0.93	0.03	0.00	0.00
30856	predictable	1.098	1.09345	0.85	0.00	0.05	0.92	1.00
30815	predictable	0.9044	1.10994	1.00	0.28	0.00	0.72	1.00

(*Continued*)

Table S1: continued

Fish ID	Initial pattern	K1	K2	Shelter1	Shelter2	Activity1	Activity2	Exploratory
30872	predictable	0.8386	0.94616	1.00	1.00	0.00	0.00	0.00
30835	predictable	0.9525	1.02344	0.35	0.02	0.65	0.98	0.00
30889	predictable	0.928	1.10712	0.13	0.17	0.00	0.48	1.00
30830	predictable	0.9437	1.14011	0.00	0.78	1.00	0.22	0.00
30875	predictable	0.8997	1.05007	0.60	1.00	0.40	0.00	−1.00
30831	predictable	0.9178	1.04309	1.00	1.00	0.00	0.00	0.00
30884	predictable	0.9286	1.03424	0.00	0.00	0.00	0.00	0.00
30864	predictable	1.0834	1.02332	1.00	0.83	0.00	0.17	1.00
30839	predictable	0.91	1.09959	0.13	1.00	0.67	0.00	−1.00
30809	predictable	0.925	1.03764	0.87	1.00	0.10	0.00	−1.00
30804	predictable	0.9528	1.17407	0.30	1.00	0.70	0.00	−1.00
30828	predictable	0.9329	0.96948	0.03	0.70	0.07	0.18	1.00
30881	predictable	0.9913	1.00195	0.00	1.00	0.00	0.00	0.00
30822	predictable	0.8742	0.94272	0.00	1.00	0.00	0.00	0.00
30877	predictable	0.7614	0.94094	1.00	1.00	0.00	0.00	0.00
30868	predictable	0.964	0.69098	1.00	0.82	0.00	0.18	1.00
30894	predictable	0.9974	1.0514	0.57	1.00	0.43	0.00	−1.00
30858	predictable	1.0336	1.12077	0.47	0.20	0.53	0.80	0.00
30869	predictable	0.9446	1.06854	1.00	1.00	0.00	0.00	0.00

K – body condition calculated at the beginning of the experiments (K1) and at the end (K2). Shelter – proportion of the time spent in/around the shelter during the experiment (first experiment – Shelter1, second experiment – Shelter2). Activity– proportion of the time spent by fish on active movement during the experiment (first experiment – Activity1, second experiment – Activity2). Exploratory – changes in exploratory behaviour (over 10% of time active and crossing the plant barrier) between experiments; we applied a categorical scoring system: a value of +1 indicated the emergence of exploratory behaviour in the second trial (i.e., absent in the first, present in the second), −1 indicated a loss of exploratory behaviour (present in the first, absent in the second), and 0 indicated no change (behaviour either present or absent in both trials).