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The Effect of Turbidity on the Behavior of Bleak (*Alburnus alburnus*)

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Abstract: In group-living species, social interactions with conspecifics play a crucial role in group formation and the ability to make consensus decisions, with far-reaching consequences for ecological and evolutionary processes in natural populations. Individual recognition and partner preferences based on social familiarity are important mechanisms driving a range of interactions between individual fish and social structure in fish populations. However, the social interactions of gregarious species are also influenced by the ecological environment experienced by individuals. This study aimed to determine how fish shoals' structure is shaped by increased turbidity, a typical environmental constraint in anthropogenically impacted rivers. A freshwater, shoal-forming, visually orientated pelagic fish—bleak (*Alburnus alburnus*)—was used as the model organism. The behavior of 40 individuals at three different turbidity levels (0 NTU, 30 NTU, 60 NTU) was tested in the laboratory experiment. Specifically, the aim was to determine if the turbidity reduces between individual distances in response to the deteriorated visual conditions. The results showed that bleaks increased the compactness of the shoal even at the medium turbidity level (30 NTU), and compactness further increased with turbidity. Such results indicate that turbidity is an important phenomenon influencing the structure of shoals and ultimately an ecological process in natural fish populations in ecosystems affected by increasing turbidity.

Keywords: turbidity; pelagic fish; behavior; shoaling; group structure; shoal cohesion; common bleak

Key Contribution: For schooling pelagic fish, turbidity can have a major effect on shoal structure. This is the first experimental test to investigate the social interactions of pelagic fish, *Alburnus alburnus*, in various turbidity levels. We found that the bleak shoal has a more compact structure with an increasing level of turbidity, which is manifested by a reduction in the distances between individuals in the group. Such results indicated high phenotypic plasticity of bleak and an ability to adapt to anthropogenic changes in the riverine environment.

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Citation: Horka, P.; Vlachova, M. The Effect of Turbidity on the Behavior of Bleak (*Alburnus alburnus*). *Fishes* **2024**, *9*, 3. https://doi.org/10.3390/fishes9010003

Academic Editor: Will Norton

Received: 10 November 2023
Revised: 29 November 2023
Accepted: 18 December 2023
Published: 20 December 2023

1. Introduction

The social structure of animal populations is fundamental for understanding ecological and evolutionary processes in a natural population [1]. Most animals have a strong tendency to live in groups, at least for part of their life [2]. A school of fish consists of at least three or more fish that cooperate, communicate, and swim together in a group. Such collective behavior, i.e., the coordinated behavior of a group of organisms, usually increases the chance of survival and fitness of individuals in many animal species, such as schools of fish, flocks of birds, or packs of mammals [3].

From an evolutionary perspective, the main benefits of living in groups have been associated with a reduction in predation risk and an increase in predator vigilance [4,5]. Group members may benefit from improved antipredator responses via dilution effects [6], earlier predator detection [7], and coordinated group maneuvers [8], which may increase the chance of escape. Under certain situations, individuals in groups may also have better food-finding ability and improved foraging performance under predation pressure, e.g., [9,10]. Schooling has also been thought to confer hydrodynamic benefits if individuals adopt positions such that they exploit the shedding of vortex sheets from those ahead [11].

It is well known that both predator and prey species in fresh waters obtain and assess information about their environment from a variety of visual cues, and that the ability to use such cues is influenced by turbidity [12]. As a consequence of increased sediment loads, turbidity increases occur under both natural and anthropogenic conditions; however, increasing levels of turbidity caused by eutrophication, agricultural runoff, and other anthropogenic activities have become a serious ecological concern worldwide [12,13]. Human activities have profoundly altered nutrient levels in many of the world's surface waters by enormously increasing nutrient concentrations; e.g., in Western Europe, they have increased 10 to 50 times [14]. Together with river alteration, climate change, and catchment land use, excessive nutrient loading is assumed to be the most serious factor threatening freshwater biodiversity [15–17].

In lentic ecosystems, eutrophication substantially altered fish assemblage structure [18,19]. Nutrient enrichment usually leads to sustained turbidity and fundamentally reduces visibility due to the reduction in the amount of light passing through the water column [12,20]. In rivers deteriorated by anthropogenic pollution, an alteration of the visual environment may have an overwhelming ecological consequence for the whole fish community structure. For schooling in pelagic fish that serve as prey for predators, turbidity can have a major effect on shoal structure. In habitats where vision serves as the primary source of information, turbidity may lead to significant alterations in fish behavior and changes in fish species composition and densities [12,13,20,21]. For example, ide (*Leuciscus idus* L.), a benthopelagic, riverine cyprinid inhabiting deeper, slower-flowing reaches of lowland middle-sized rivers, extends their diurnal movements and home range as a result of the reduced foraging success in turbid water [13]. Although the effect of turbidity on predator–prey relationships is already well understood, its influence on the structure of shoals is not well understood, even though at least half of all species of fishes are used to living in shoals during their life [22]. Therefore, our study aimed to test how the behavior of pelagic fish, namely shoal structure, changes in different turbidity levels.

For our study, we chose common bleak, *Alburnus alburnus* L., as a model fish. The reason was that bleak, as a smaller pelagic fish, creating large populations in the river environment, is an important part of the food chain as prey for predators. Moreover, bleak is an obligate schooler [23,24]. Bleak is a mobile, visually orientated pelagic fish [23,25] inhabiting lakes and rivers across Europe [26,27], which usually occurs in shoals [24]. Bleak is a day-active plankton feeder [28–30] and bleak itself constitutes an important prey species for several species of fish predators [31]. In the absence of conspecifics, bleaks display increased motoric activity and join other fish until conspecifics are again encountered [32]. When a school of bleak encountered a group formed by another species, it retained its cohesiveness and feeding technique; this species did not form aggregations with other fishes [23]. Bleaks face strong predator pressure and forming groups is an effective strategy to avoid predation, especially in open-water habitats. For bleaks, prey is often sparsely distributed, which may reduce foraging competition, which in turn suggests that shoaling and various social interactions in bleaks may be a strategy to cope with predation threat in particular. However, the expression of such behavioral associations in individuals and hence the behavior of bleak shoals will be undoubtedly shaped by various external factors, which may further influence the overall behavioral response [2,8,33].

Investigating the impact of turbidity on freshwater fish helps to understand how changes in water clarity can affect fish populations and is vital for developing conservation strategies to protect and preserve biodiversity in rivers and lakes. In our study, we tested a prediction: that the behavior and the structure of bleak shoal are influenced by an environmental constraint presented by increased turbidity. We predicted that in the treatment with increased turbidity, the distance between individuals in the group will decrease because the fish will gradually lose visual information from their surroundings as the water turbidity increases. We also assumed that at a medium level of turbidity the visual perception will not be disturbed enough to cause changes in the structure of the fish shoal and that only high turbidity will have a demonstrable effect on the behavior of the bleaks, as the visual perception will be strongly disturbed by turbidity.

2. Materials and Methods

2.1. Experimental Design

For the experiment, we captured adult bleak (*Alburnus alburnus*) from the River Berounka in the Czech Republic. A total of 40 individuals were caught. The Berounka River is the largest left-hand tributary of the Vltava River, which empties into the Vltava River in the territory of Prague near Lahovice, 194 m a. s. l. (49°58.565′ N, 14°21.614′ W). It originates in Pilsen, at the confluence of the Mže and Radbuza River, its length is 139.1 km, with the longest source (Radbuza-Uhlava) 252 km. The bleaks were caught by fishing using a rod. After the catch, the fish were carefully placed in an aerated barrel and transported to the Fish Ecology Laboratory at the Institute for the Environment. Immediately after the transfer, the fish were placed in two pre-prepared aquariums with a volume of 430 L (habituation aquariums). Here, the fish were left for 4 weeks to acclimate fish to laboratory conditions gradually. Fish were fed daily frozen mosquito larvae ad libitum during acclimatization. The aquariums were equipped with external filters with aeration. The mean water temperature was 15.42 °C with a natural daylight regime. In the experiment, 40 individuals were used, which were randomly divided into 8 groups, each representing a shoal with 5 individuals. When determining the number of fish used in our experiments, we followed the ethical standards and regulations governing the use of animals in research and the 3R rule, i.e., reducing the number of fish per trial to a minimum while maintaining a sufficient amount of data for statistical analysis and sufficient space for fish to exhibit natural shoaling behavior. This also minimizes the likelihood of shoaling by chance due to the size constraints of an observation tank. For each of the eight groups, each level of turbidity (0 NTU (control), 30 NTU, 60 NTU) was prepared and measured. To control for potential order effects due to exposure to different turbidity levels, the order of exposure to different turbidity levels was randomly assigned for different experimental groups. Each group experiences the same total duration of exposure but in a randomized sequence. The average size of the individuals was 13.7 ± 1.3 cm SL (SL, Standard Length ± S.D.).

Turbidity levels were chosen according to the turbidity values commonly observed in Czech rivers, and graduated to cover low, medium, and high turbidities, namely 0 NTU, 30 NTU, and 60 NTU (Nephelometric Turbidity Units (NTU)). The suggested degrees of turbidity were based on data on water quality in Czech rivers derived from long-term monitoring of nutrient concentrations by the Czech Hydrometeorological Institute ČHMÚ (http://www.chmi.cz, accessed on 30 November 2019), which conducts monthly monitoring at sampling sites. Turbidity values were determined and measured using a WTW Turb 355 T turbidimeter (https://www.wtw.com, accessed on 30 January 2020). The device measures the beam intensity and evaluates the degree of turbidity level of the measured sample. To prepare turbid water, we used pre-prepared clay, which we let dissolve gradually in the aquarium. Subsequently, we mixed the water with the dissolved clay in such a way that the required turbidity value was created in the entire aquarium, which we checked through three measurements in different places in the aquarium.

During the experiment, the individuals were placed in the experimental tank, where their behavior was monitored from the top using a camera (GoPro Hero 10 https://gopro.com, accessed on 10 April 2020), with a resolution of the main lens of 23 MPx. The experimental aquarium was located separately from the aquariums where the fish were left for 15 min for acclimatization, followed by an 8 min record. Together with turbidity, temperature and fish length were measured during each experiment. For the experiment, the water level was lowered to 11 cm, as it would not be possible to distinguish individuals from each other at higher water levels. Before being filled with water, the experimental aquarium was divided using a black marker into a regular square grid of 10 cm × 10 cm. The grid was outlined along the entire bottom of the aquarium, and only vertical lines of

10 cm were drawn on the sides, which connected to the bottom square grid. Each of the eight groups experienced each turbidity treatment. Particular groups were tested only once within one day. After the video recording was made, the experimental tank was washed with clean water and filled again with fresh water. At the end of the experiment, the fish were transported back to the place where they were originally caught and released at the site of capture.

All institutional and national guidelines for the treatment of experimental animals (Act No. 246/1992) were followed during the experiment. The experimental project was approved by the Ethics Committee of the Faculty of Natural Sciences of Charles University in Prague.

2.2. Video Processing

The camera images of each subgroup that had just finished the experiment at each turbidity level were stored on the computer in an assigned folder that belonged only to that subgroup. The beginning and end parts of four minutes were cut from each video. The video recorded in this way was used to evaluate the behavior of the fish. The evaluated videos were 8 min long. Images (screenshots) were created from these video recordings, which followed each other for ten seconds. Images were evaluated using ImageJ 1.52f (https://imagej.nih.gov/ij, accessed 10 April 2020 [34]). Using a connecting line, the mutual distances between individual fish in the experimental aquarium were measured for each monitored group (10 values for each measurement after 10 s). Distances between individuals were measured as a straight line from the mouth opening of the individuals. As the camera's location in the center above the aquarium distorted the captured image, the distances between the individuals in the used program were calibrated using the square grid on the bottom of the aquarium and only measured with a connecting line after calibration. A total of 11,600 measured values were obtained at 3 degrees of turbidity. The characteristics of the basic set of measured data are shown in Table 1.

Table 1. The experimental design was inter-individual distance × turbidity × temperature × group ID × fish length.

Variable Name	Variable Type	Variable Impact
Inter-individual distance (n = 11,600)	Numeric	Dependent
Turbidity (n = 3)	Numeric category	Independent
Group ID (n = 8)	Category	Random
Temperature	Numeric	Random
Fish length (n = 40)	Numeric	Random
Number of fish per group (n = 5)		

2.3. Statistical Analysis

Results were evaluated using R 4.0.5 (R Core Team, 2021 [35]). Linear models were used to test the differences in group behavior at various turbidity levels (Table 1). Data were log-transformed to meet the assumption of normality and homoscedasticity of variances. Inter-individual distances and turbidity were treated as fixed effects. Individual groups of fish and temperature were included as random effects in the analysis. To test the differences between degrees of turbidity, analysis of variance (ANOVA) was used. As part of the evaluation of the results, we also checked whether the distance at different degrees of turbidity differed between individual groups and different temperatures and fish lengths.

3. Results

A total of 11,600 measured values were obtained at three degrees of turbidity (Table 2). The effect of turbidity levels on the behavior of bleak is shown in Table 2. The average water temperature in a tank during the experiment was 15.42 ± 2.01 °C (mean ± S.D.). The water temperatures during the individual experiments were subsequently used in statistical comparisons as a random factor. The mean inter-individual distances at the 0 NTU level were 20.7 cm, which decreased by 1.3 cm at the 30 NTU and 3.7 cm at the 60 NTU.

Table 2. The effect of turbidity levels (NTU—Nephelometric Turbidity Units) on the inter-individual distances of bleak (*Alburunus alburnus*) shoal.

Turbidity (NTU)/ Distances (cm)	Min. (cm)	1st Qu (cm)	Median (cm)	Mean (cm)	3rd Qu. (cm)	Max (cm)
0 NTU	1.2	12.8	18.9	20.7	26.3	101.4
30 NTU	0.6	11.8	17.1	19.4	24.3	108.8
60 NTU	0.2	9.4	14.4	17.0	21.5	105.9

The result of the model showed significant differences in the inter-individual distances of fish under various levels of turbidity (Figure 1). The inter-individual distance differed significantly by turbidity (mixed model: $F_{1,2} = 51.6$; $p < 0.001$) and by group ID ($F_{1,7} = 4.15$; $p < 0.001$), but not by temperature ($F_{1,23} = 3.85$; $p = 0.05$) or fish length ($F_{1,23} = 0.01$; $p > 0.05$).

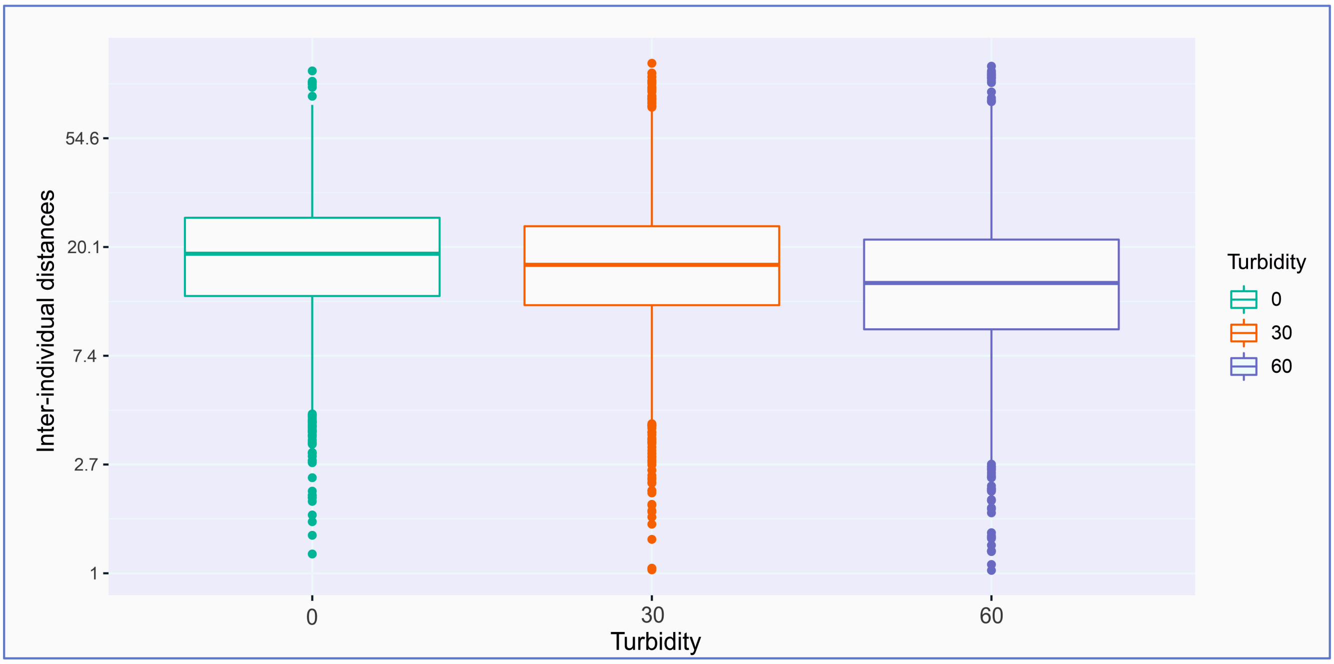

Figure 1. Inter-individual distances of bleak (*Alburnus alburnus*) in different turbidity levels (NTU—Nephelometric Turbidity Units).

At the lowest turbidity levels (0 NTU), the differences between the groups were not statistically significant ($F_{1,7} = 0.302$, $p > 0.05$); similarly, no significant differences between the groups were found at the highest turbidity level, at 60 NTU ($F_{1,7} = 1.164$, $p > 0.05$). On the contrary, at the medium turbidity level (30 NTU), significant differences were found in the inter-individual distances of fish between groups ($F_{1,7} = 4.15$, $p < 0.001$).

4. Discussion

Fish schooling is a phenomenon of long-lasting interest in ethology and ecology [36]. In fish, shoals represent an important form of social organization. Since they can be readily observed and manipulated, fish represent an excellent opportunity to quantify the behavior of individuals and link them to higher-order properties at the group and population levels [3]. In our study, we tested a prediction: that the behavior and the structure of bleak shoal are influenced by an environmental constraint presented by increased turbidity. Under these conditions, the fish in the shoal usually clump together and form a more compact structure [3].

Our results show that the shoal responds to increased turbidity by reducing the inter-individual distances within the shoal, with increasing shoal cohesion with increasing levels of turbidity. Such changes in fish behavior can be caused by proximal factors, i.e., factors that primarily determine such behavior. This can be mainly a deterioration in visual acuity in fish, where impaired visual acuity reduces the fish's response to its surroundings [37]. For example, the emerald shiner *Notropis atherinoides*, due to deteriorated visual acuity in increased turbidity conditions, reduce their distance so that they can better see the individuals in the shoal [38]. Bleaks are small fish, but their eye-size-to-body-size ratio is relatively high, which may facilitate adaptation to turbid environments. At the same time, this also means that visual perception is essential for the bleak, and therefore turbidity can have a considerable effect on the bleak. Our findings that shoal cohesion is more compact even at the middle level of turbidity, 30 NTU, corresponds with possible effects on vision in bleak.

Ultimately, increased shoal cohesion in high turbidity may be caused by an impaired ability to communicate between individuals and protect against predators [39]. Although the increased cohesion of the shoal makes it easier to recognize and react to the presence of a predator in poor visual conditions, there are also disadvantages to being a shoal member. Aggregations may be more conspicuous to predators, with the likelihood of detection increasing with shoal size [33]. Moreover, levels of competition for resources are expected to be elevated in groups [2,8], and there is also the potential for faster spread of directly transmitted parasites [40]. The deterioration in visual conditions also changes the choice of prey for certain predators, who, thanks to reduced visibility, can reach prey that they would not even have a chance to detect under favorable visual conditions because the prey would have the opportunity to escape [41]. This can be especially true for fish that can see the bleak at increased levels of turbidity, i.e., in a situation where the bleak cannot see the predator due to impaired vision, or only at a short distance, while the predator can see the bleak shoal before via some kinds of adaptation. The increased cohesion of bleak shoal found in our study thus further supports and emphasizes the importance of the advantages that life in groups provides, e.g., [42,43]. Among the most pronounced can be predator vigilance, which result from an increased chance of one or some group members detecting predators, the so-called many-eyes effect [44], and mechanisms allowing fast information transfer across the school, the so-called Trafalgar effect [45].

Common pike (*Esox lucius* L.), pikeperch (*Stizostedion lucioperca* L.), or European catfish (*Silurus glanis* L.) are typical predators of bleaks and especially asp (*Leuciscus aspius*, Linnaeus 1758), for which bleaks become a preferred diet [31,46,47]. Among them, the pikeperch is a predator with an increased ability for visual perception under low light intensities [48] and could therefore take advantage of the fact that the shoal is more compact. Therefore, it depends not only on the adaptation of the visual perception of the bleaks but also on their predators.

Prey fish typically respond to the presence of predators by increasing the time spent in schools and controlling predator activity [49,50]. Higher threat from predators leads to more synchronized group movement, with the speed of nearest neighbors increasing and the distribution becoming more compact [51]. In our case, the shoals were more compact even without the presence of a predator. Such behavior could suggest that turbidity significantly affects the behavior particularly due to the reduced visibility, and that directly proximate factors play a role in the behavioral response of bleaks. Such results also indicate high phenotypic plasticity of the bleak and, therefore, a high ability of this species to adapt to anthropogenic changes in the riverine environment.

We assumed that a medium level of turbidity (30 NTU) would not induce a significant difference in inter-individual distance among individuals in the shoal, as the visual perception would not be disturbed enough to cause changes in the shoal structure. However, it has been shown that even a medium level of turbidity causes an effect, suggesting that visual perception is disturbed even at lower levels of turbidity (30 NTU). Although there was a significant shift in shoal cohesion between levels 0 NTU and 30 NTU, there were also significant differences between individual groups at the turbidity level of 30 NTU. Such findings may suggest that a turbidity level of 30 NTU is a level where some groups are still capable of good visual perception and others are not. The behavior and sensitivity of fish to turbidity depend on the degree of turbidity, species-specific reactions, and tolerance to water turbidity [52–54]. It has been shown that some fish species, such as the bridle shiner (*Notropis bifrenatus* Cope 1867) and the long-nosed fawn (*Notropis anogenus* Forbes 1885), even at a low water turbidity <10 NTU, change their schooling behavior as a result [53]. Michael et al. [55] examined if water clarity would alter collective movement in the red shiner (*Cyprinaella lutrensis*) and sand shiner (*Notropis stramineus*) in up to 200–300 NTU. They found decreased collective behavior in response to turbidity indicated by significant increases in inter-fish distances. This is in contrary to our results; however, [55] exposed fish to a high degree of turbidity, where fish were not able to detect one another. The specific behavioral threshold in response to turbidity levels may also vary between individuals of wild and hatchery origin. For example, in the study of Horka et al. [21], it was shown that the wild grayling *Thymallus thymallus* (L.) shows threshold behavioral response to increased turbidity levels, probably as a result of a trade-off between movement and feeding efficiency at different turbidity levels. In contrast, the unterminated behavioral response found in the hatchery-reared *T. thymallus* could be viewed as a result of a lack of juvenile experience in rivers [56].

5. Conclusions

Rivers are currently being degraded by several negative anthropogenic factors such as flow regulation, increased pollutant inputs, and the effects of climate change. The result is a global reduction in the ecological quality of fish communities [57–59] and the disruption of river ecosystems, which are currently among the habitats most at risk of loss of biodiversity [60–62]. One of the anthropogenic factors that fundamentally affect fish communities in flowing waters is the increased supply of nutrients, resulting in an increase in environmental turbidity [12,63]. Climate change can influence precipitation patterns, leading to changes in river flow and sediment transport, which may further contribute to increasing turbidity levels. In an environment where visual perception is the primary source of information, increased turbidity values can lead to substantial changes in fish behavior up to a total change in the structure and function of fish communities [12,13]. Our results suggest that even lower turbidity values can affect the structure of pelagic fish shoals. This proves that turbidity is a phenomenon that affects ecological processes in natural fish populations living in ecosystems affected by increasing turbidity. Our findings thus highlight the need for the restoration of natural habitats and adjacent buffer zones of riverine habitats [64], which would advance efforts to reduce agricultural runoffs and other sources of nutrient pollution to water habitats and mitigate and prevent further degradation of aquatic environments.

Author Contributions: Conceptualization, P.H.; data curation, M.V.; formal analysis, P.H. and M.V.; methodology, P.H. and M.V.; writing—original draft, P.H.; writing—review and editing, M.V. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: The animal study protocol was approved by the Institutional Ethics Committee of CHARLES UNIVERSITY (protocol code 19014/2019-MZE-18134 and 3 April 2019) for studies involving animals.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data are available at Figshare data repository (https://figshare.com/account/items/24541153/edit, accessed on 20 November 2023).

Conflicts of Interest: The authors declare no conflict of interest.

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