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# Turbidity reduces territory defence and exploration in an East African cichlid, *Neolamprologus pulcher*

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Human activities increase turbidity in aquatic environments worldwide, which often affects fish behaviour. However, predicting how species react to higher turbidity remains difficult, as responses vary depending on the species, their ecology and the ecosystem. It is thus important to improve our understanding of the responses of fishes living in ecosystems experiencing recent increases in turbidity, especially those with unique species compositions where biodiversity is most vulnerable. One such ecosystem is Lake Tanganyika in East Africa, which is home to a diverse fish community with a high degree of endemism. In this study, we conducted a laboratory experiment with the territorial cichlid, *Neolamprologus pulcher*, which is endemic to Lake Tanganyika, to investigate the effects of increased turbidity on territorial and exploratory behaviour. We found that moderate increases in turbidity led to reduced territory defence, decreased exploration and increased time spent in shelters. Given that these fish live in large colonies, feed on planktonic particles in the water column and defend their territory against conspecific and heterospecific intruders, these behavioural changes are likely to have substantial implications for their social structure and reproduction in their native environments. Our study raises important questions about whether these effects will persist in the long term as human activities are likely to continue to increase turbidity in the lake over the coming decades and whether the responses to turbidity affect the community composition of fishes in Lake Tanganyika.



Human activities, such as deforestation, agriculture and shoreline habitat alterations, increase turbidity (that is, reduced visibility caused by suspended particles) in aquatic ecosystems globally, which frequently affects fish behaviours (Henley et al., 2000; Horka & Vlachova, 2024; Smith, 2003). Some fish species respond by moving away from degraded habitats and altering their movement and activity patterns (Gray et al., 2011; Rodrigues et al., 2023). For less mobile species that cannot relocate to undisturbed habitats, increased turbidity can have far-reaching consequences, including reduced reproductive success and changes in mating behaviour that may lead to the loss of biodiversity through reverse speciation (Engström-Öst & Candolin, 2007; Järvenpää et al., 2019; Seehausen et al., 1997, 2008; Sundin et al., 2010; Vonlanthen et al., 2012). Many fish species also show more subtle behavioural responses to increased turbidity and subsequent reductions in visibility, such as changed shoaling behaviour, courtship, foraging, predator–prey interactions, reduced predator perception and territory defence (Borner et al., 2015; Candolin et al., 2007; Fischer & Frommen, 2013; Henriksson & Candolin, 2020; Horka & Vlachova, 2024; Leahy et al., 2011; Michael et al., 2021; Ortega et al., 2020; Zanghi et al., 2023). The direction and strength of these responses vary by species, their ecology and habitat, making general predictions difficult (Rodrigues et al., 2023). Therefore, it is important to explore the responses of fish species native to habitats experiencing increased turbidity, particularly in less mobile species with small geographical ranges.

Lake Tanganyika hosts an important fish community that is characterized by a high degree of endemism and a small geographical range, which is affected by increased turbidity (Phiri et al., 2023). The lake is home to at least 241 cichlid fish species (98% endemism) and 150 species of non-cichlid fishes (56% endemism; Ronco et al., 2020). It is recognized as an important and

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threatened biodiversity hotspot that should be a priority for conservation efforts (Groombridge & Jenkins, 1998; Ronco et al., 2020; Salzburger et al., 2014; Sturmbauer et al., 2009). The most species-rich habitat is the littoral shoreline, down to a depth of 40 m (Takeuchi et al., 2010). These habitats are particularly exposed to the consequences of human activities on land. Historically, Lake Tanganyika has maintained clear water with turbidity levels ranging from 0 to 15 nephelometric turbidity units (NTU). However, like in many other lakes worldwide, large-scale deforestation has led to increased sediment loads being discharged into the lake (Alin et al., 2002; Britton et al., 2017; Cisternas et al., 2001; O'hara et al., 1993; Shen et al., 2022; Sichingabula, 1999). Consequently, visibility has decreased in several areas due to the river inflow of suspended particles during the rainy season and due to eutrophication (Moshi et al., 2022; Shen et al., 2022; Yu et al., 2018). Although these changes may affect many aspects of fish behaviour in the coastal areas of the lake, very little is known about how species native to the lake react to changes in turbidity.

An endemic cichlid species of Lake Tanganyika that is well suited to investigate the responses of cichlids to increased turbidity is the Princess of Burundi, *Neolamprologus pulcher*. This species is widely distributed along the lake shores, predominantly inhabits depths of 3–40 m and feeds on pelagic plankton (Duftner et al., 2007; Gante et al., 2016; M. Taborsky & Limberger, 1981). *N. pulcher* is highly social and both sexes defend territories that are the home of 1–40 individuals (Balshine-Earn et al., 1998; Hellmann & Hamilton, 2018; Jungwirth & Taborsky, 2015; Jungwirth et al., 2023). These territories are part of large colonies, where the cichlids use a variety of visual displays and aggressive behaviours to defend against conspecific intruders (Balzarini et al., 2017; Culbert & Balshine, 2019; Desjardins et al., 2008). Territory owners breed in small cavities between rocks, with some group members assisting in brood care (Taborsky & Limberger, 1981; Zöttl, Fischer, & Taborsky, 2013; Zöttl, Heg, et al., 2013). Due to their cooperative breeding and colonial territorial structure, *N. pulcher* has become a model species for studying fish social behaviour (Taborsky, 2016; Wong & Balshine, 2011), with standardized behavioural assays established for quantifying behaviours, such as territory defence and exploration (Balzarini et al., 2014; Chervet et al., 2011; Schurch & Heg, 2010b).

In this study, we conducted a laboratory experiment to investigate how *N. pulcher* responds to moderate increases in turbidity, that is, levels found well within the natural range found in Lake Tanganyika (Langenberg et al., 2002; Plisnier et al., 1999). We used bentonite clay to increase turbidity in the treatment group to around 4 NTU while maintaining control observations at levels below 1 NTU (Illing et al., 2024; Leris et al., 2022; Ranåker et al., 2012). Our behavioural assays focused on quantifying territorial defence by measuring the fish's responses to mirrors and assessing boldness using an established exploration paradigm (Balzarini et al., 2014; Schurch & Heg, 2010a). We predicted that increased turbidity impairs the vision of cichlids and decreases the efficiency at which cichlids can use visual displays towards conspecifics and heterospecifics, leading to changes in their ability to defend their territories. Additionally, we hypothesize that impaired vision would make *N. pulcher* more risk-averse, less exploratory and more shelter-seeking, as predators will be spotted at shorter distances.

## METHODS

### *Subjects and Holding Conditions*

We used cichlids, *N. pulcher,* that originate from wild individuals caught in Lake Tanganyika near Mpulungu, Zambia, in the years 1999, 2006, 2009 and 2020. In the laboratory, they were maintained in breeding groups and stockholding tanks at a temperature range of 26–27 °C with a 13:11 h light:dark photoperiod. The tanks were equipped with commercial air-driven sponge filters (XY-2822) and 1–2 heaters, and the bottom was covered with a layer of sand (grain size 0.1–0.5 mm). The water was treated with 0.4 g Sera GH/KH-plus and 0.067 g sodium bicarbonate per litre before use. All fish were fed once a day, 6 days per week, using commercial food flakes (Tetra, Osnabruck, Germany). On experimental days, we fed the experimental subjects after the last observations.

### *Experimental Procedure*

We haphazardly selected 36 individuals (18 females, mean ± SD standard length: 5.54 ± 0.72 cm; 18 males, 5.41 ± 0.53 cm) from various stock tanks. We placed each of them into one of two compartments of 222 litre tanks (45 × 110 × 45 cm, Fig. 1). An opaque polyvinyl chloride (PVC) sheet divided the compartments. Each compartment included one flowerpot half, which the fish quickly accepted as the centre of their new territory, indicated by the fish frequently using it as a refuge. All fish were placed in the experimental compartments 48 h before the start of the experiment to ensure that they had fully settled in their new environment.

To investigate the effect of turbidity on cichlid behaviour, we adopted a within-subject experimental design. Each of our experimental subjects was tested in the control condition (turbidity mean of two measurements before the mirror assay = 0.61 NTU ± 0.23 SD; range 0.33–1.15; and before the exploration assay = 0.68 NTU ± 0.34 SD; range 0.3–2.2) and in a treatment where we used bentonite clay to increase the turbidity (mean before the mirror assay = 4.73 NTU ± 0.86 SD; range 2.8–6.3; and before the exploration assay = 3.15 NTU ± 0.43 SD; range 2.30–4.05). To achieve this level of turbidity, we suspended 4 g of bentonite clay in 200 mL of water and added this suspension to the experimental tanks. A pilot trial indicated that adding this suspension initially elevated the turbidity to 6 NTU and that subsequent sedimentation led to a gradual decrease of turbidity

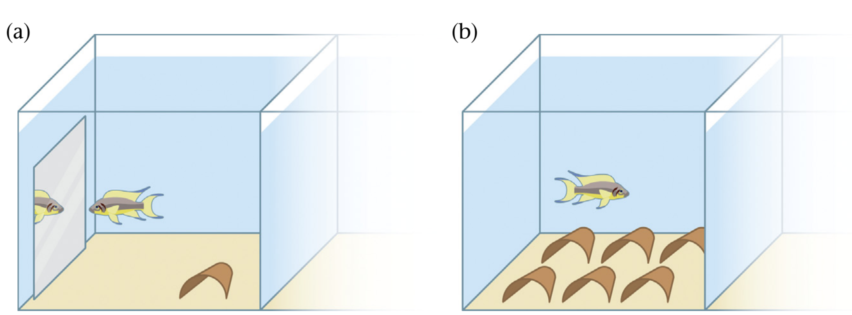


**Figure 1.** The experimental set-up in subdivided tanks with two compartments during (a) the mirror test and (b) the exploration test.

to 2—3 NTU during 1 h. In the control condition, we added 200 mL of water to the tanks without suspending the bentonite clay before adding the water to have the same chemical properties and disturbance in the turbid treatment and clear control. Half of all subjects underwent the treatment first and 1 day later the control, whereas in the other half, we reversed this order. To measure turbidity, we collected water samples in 50 mL Falcon tubes for each individual before each behavioural assay and measured turbidity with a WTW Lab Turbidity Meter Turb 550 IR.

We tested each subject for their investment in territorial defence by using a mirror assay (Balzarini et al., 2014) and for their tendency to explore the territory by using an exploration test (Fig. 1; Schurch & Heg, 2010a). We started the mirror test 10 min after adding the turbidity suspension or the control water by placing a 15 × 22 cm mirror inside the tank. Subsequently, we conducted 10 min of all-occurrence sampling of aggressive display behaviours (head down, frontal display, lateral display, S-bend) and of overt attacks (ramming, biting, bow-swim) against the mirror (Balzarini et al., 2014; Culbert & Balshine, 2019; Reddon et al., 2019). After a break of 15 min, we added 5 new flower pots to the territory of the cichlid and started immediately to record their exploratory behaviour for 10 min. During this 10 min, we recorded each time the focal fish entered or left a pot and subsequently derived the latency leaving the first pot, the number of unique pots visited, the total number of pots visited, the time spent outside pots, mean distance per pot jump and total distance covered. All observations in both assays were carried out by the same observer sitting 1 m from the tank, logging all events in real time on a laptop running BORIS event-logger (Friard & Gamba, 2016).

### *Statistical Analysis*

The different display behaviours and overt aggressive behaviours were combined into two separate response variables: the number of restrained aggressive behaviours (sum of head-downs, frontal displays, lateral displays and S-bends) and the number of overt attacks (sum of ramming, biting and bow-swimming). We used paired nonparametric Wilcoxon signed rank tests to test for behavioural differences between control and treatment. To see if sex affected the behavioural response, we calculated the difference in behaviours between treatment and control for each individual. We then used Wilcoxon signed rank tests to assess if the responses differed between males and females. As latency, we defined the time it took for a fish to exit the pot at the start of the exploration test. This variable could only be calculated for the 15 fish in a pot at the onset of the observation in both the treatment and the control groups, and we presented the data for these cases. To score exploratory tendency, besides the number of visited pots and the number of unique pot visits, we calculated the total covered distance while exploring based on the sequence of visited pots (Fig. S1). The level of turbidity in both the control and treatment varied due to how much the previously added clay had sedimented or the currently added clay kept being suspended. To see if this difference in the magnitude of turbidity change was associated with the strength of the treatment effect, we performed a linear regression for each response variable. Because the data of one fish in the exploration test got lost, the sample size is $N = 35$ for this test.

All data manipulation, statistical analyses and figure creation were performed using the software R Version 4.3.3 (R Core Team, 2024) with packages 'tidyverse' (Wickham et al., 2019) and 'ggpubr' (Kassambara, 2023).

### *Ethical Note*

The experiments were conducted at Linnaeus University, Kalmar, in June and July 2024 under the ethical approval of the Swedish Board of Agriculture, Linköping (DNR 19719-2023). We followed the ASAB/ABS Guidelines for the treatment of animals in behavioural research (ASAB Ethical Committee/ABS Animal Care Committee, 2023) and the principles of the three Rs by reducing stress through noninvasive test paradigms and reducing handling times to a minimum. During the experiments, the fish showed no indication of acute stress, pain or suffering; the experiments did not cause injuries or death. We monitored the subjects' wellbeing throughout the experimental period daily, and we would have

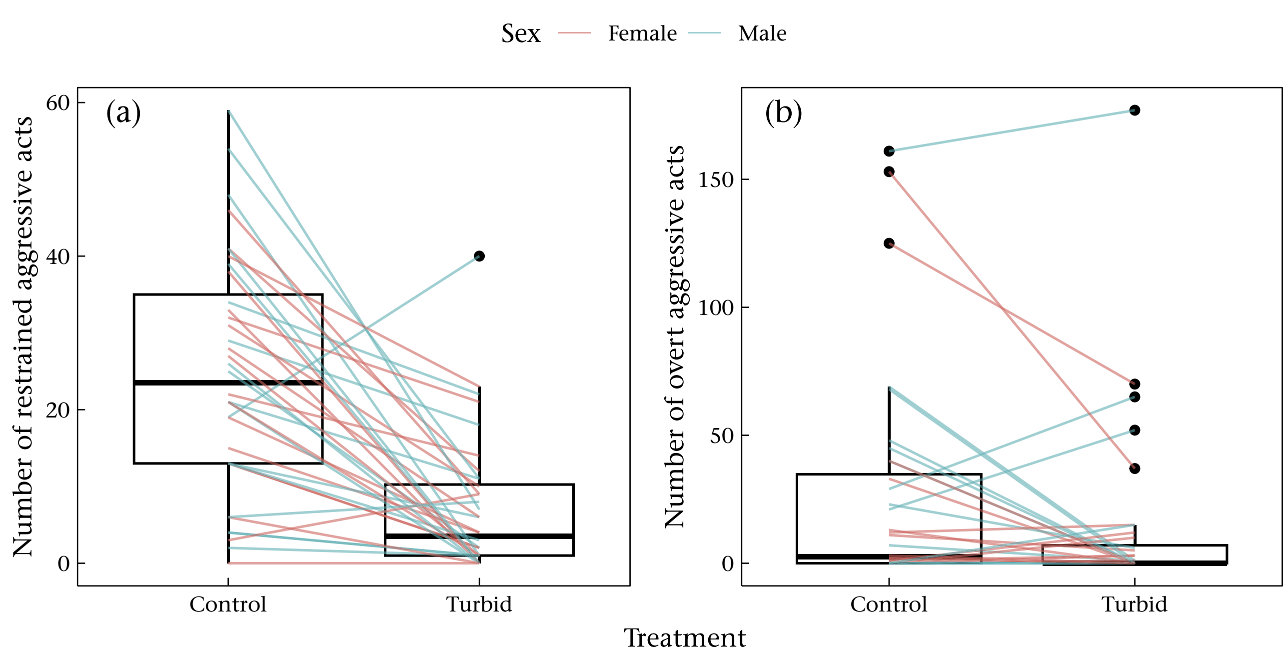


**Figure 2.** The effects of increased turbidity on (a) restrained and (b) overt aggression of $N = 36$ individuals of *Neolamprologus pulcher*. The lines connect the data points for each fish across treatments and the colours indicate their sex. The box displays the median and IQR; whiskers indicate maximum (Q3 + 1.5 IQR) and minimum values (Q1 − 1.5 IQR); and dots represent outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

aborted any experiments if the fish were at risk of acute stress and pain, incurring lasting injuries or dying. After the experiments, we returned all the fish to their holding tanks.

## RESULTS

### *Fish in Turbid Water Show Reduced Territory Defence and Explore Less*

Individuals in turbid water showed less territory defence than individuals in clear water (paired Wilcoxon signed rank test, restrained aggression: $W = 28.5$, $P < 0.001$; overt aggression: $W = 107.5$, $P = 0.052$, $N = 36$; Fig. 2a and b). In the exploration test, they started to explore their tank later, visited fewer pots and spent less time outside the pots, and although they did not shorten the mean distance between their pot visits, they travelled a shorter total distance when the water was turbid (paired Wilcoxon signed rank test, latency: $W = 25$, $P = 0.048$, $N = 15$; pot visits: $W = 179.5$, $P = 0.024$, $N = 35$; unique pot visits: $W = 418$, $P = 0.04$; $N = 35$; time outside: $W = 449$, $P = 0.028$, $N = 35$; mean distance travelled per pot jump: $W = 244.5$, $P = 0.37$; $N = 35$; total distance travelled: $W = 419.5$, $P = 0.038$, $N = 35$; Fig. 3a–d, Fig. 4a and b).

### *No Effects of Sex or the Magnitude of the Change in Turbidity on Territory Defence and Exploration*

The cichlids did not show sex-specific responses to turbidity in territorial defence (Wilcoxon signed rank test, restrained

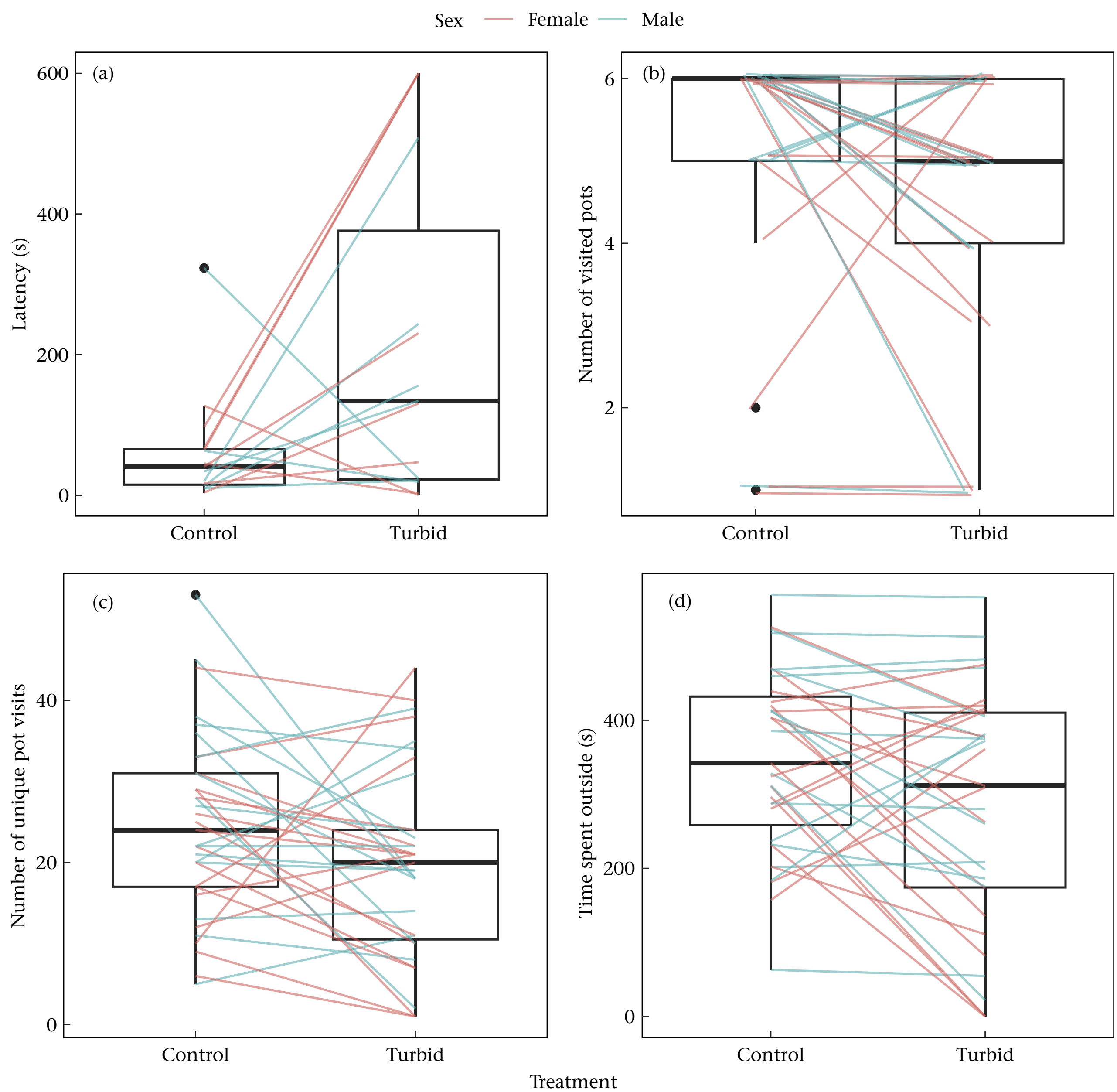


**Figure 3.** The effects of increased turbidity on (a) the latency to explore (seconds until exiting the pot), (b) the number of visited pots, (c) the number of unique pot visits and (d) the time spent outside any pot in *Neolamprologus pulcher*. The sample size was $N = 15$ individuals for latency and $N = 35$ individuals for the rest of the explorative assays. The lines connect the data points for each fish across treatments and the colours indicate their sex. The box displays the median and IQR; whiskers indicate maximum (Q3 + 1.5 IQR) and minimum values (Q1 − 1.5 IQR); and dots represent outliers. Note that the lines are jittered in (c). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

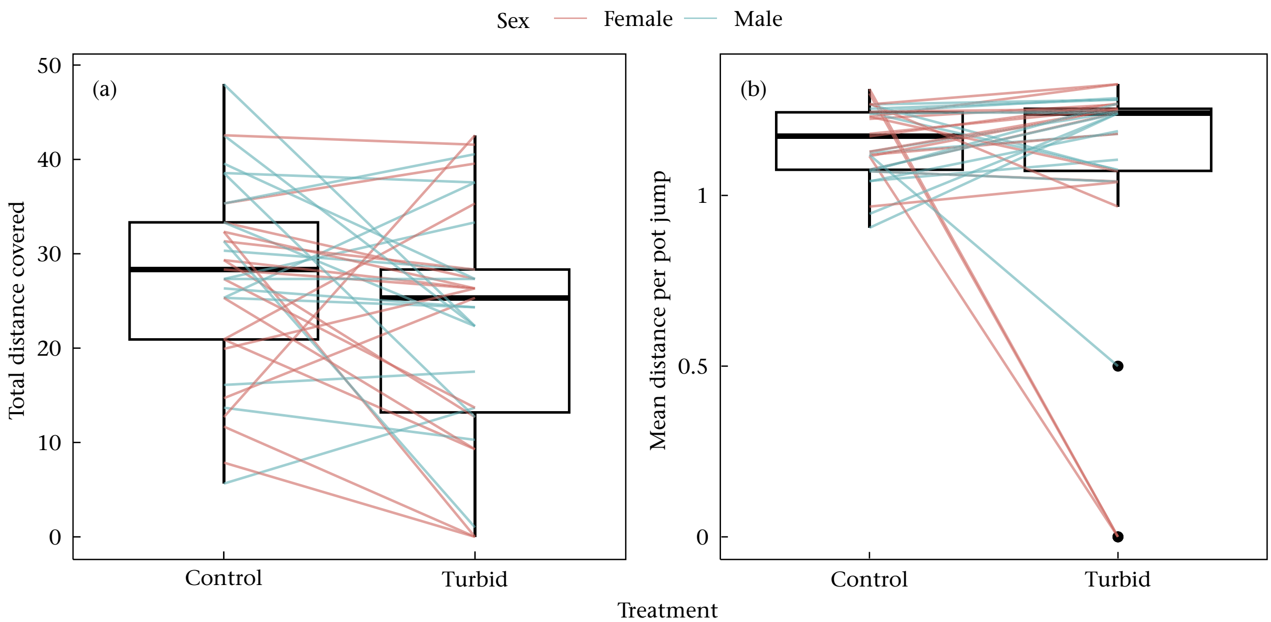


**Figure 4.** The effects of increased turbidity on (a) the total distance covered between all explored pots and (b) the mean distance between each pot visit. Distance is expressed in arbitrary units with one unit representing the distance between two adjacent (nondiagonal) pots in the 2 × 3 grid. The sample size was $N = 35$ individuals. The lines connect the data points for each fish across treatments and the colours indicate their sex. The box displays the median and IQR; whiskers indicate maximum (within Q3 + 1.5 IQR) and minimum values (within Q1 − 1.5 IQR) and dots represent outliers. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

aggression: $W = 164$, $P = 0.96$; overt aggression: $W = 162$, $P = 1$, $N = 36$) nor in exploratory behaviours (Wilcoxon signed rank tests, latency: $W = 20$, $P = 0.40$, $N = 15$; pot visits: $W = 171$, $P = 0.55$, $N = 35$; unique pot visits: $W = 158.5$, $P = 0.87$, $N = 35$; time spent outside: $W = 172$, $P = 0.55$, $N = 35$; mean distance travelled per pot jump: $W = 177$, $P = 0.44$, $N = 35$; total distance travelled: $W = 156$, $P = 0.93$, $N = 35$). Similarly, the magnitude of the turbidity change between treatments did not affect territorial defence (linear regression, restrained aggression: $F_{1,34} = 0.03$, $P = 0.86$; overt aggression: $F_{1,34} = 0.01$, $P = 0.93$, $N = 36$) or the exploratory behaviour (linear regression, latency: $F_{1,13} = 0.10$, $P = 0.76$, $N = 15$; the number of visited pots: $F_{1,33} = 1.15$, $P = 0.29$, $N = 35$; unique pot visits: $F_{1,33} = 0.15$, $P = 0.70$, $N = 35$; time outside: $F_{1,33} = 0.04$, $P = 0.85$, $N = 35$; mean distance travelled per pot jump: $F_{1,33} = 0.11$, $P = 0.75$, $N = 35$; total distance travelled: $F_{1,33} = 0.01$, $P = 0.91$, $N = 35$; Fig. S2).

## DISCUSSION

In this study, male and female cichlids were less aggressive in defending their territory and explored their tank more cautiously in turbid conditions. Fish displayed threshold behavioural responses, as the severity of the turbidity variations in the treatment (ranging from 2.8 to 6.3 NTU) did not affect the strength of their reactions. Our results show that even small increases in turbidity can have measurable and predictable effects on behaviour. Despite a large behavioural variation between individuals, which aligns with earlier findings in *N. pulcher* (Schurch & Heg, 2010a; Schurch et al., 2010), we observed consistent responses to decreased activity across both behavioural assays. The results of this study offer insight into how cichlids of Lake Tanganyika may respond to increases in turbidity in their habitat.

Previous studies have shown the contrasting responses of different fish species to changes in turbidity, making it difficult to make general predictions about the expected responses of specific species. Some species compensate for reduced visibility by increasing antipredator behaviour, which, as observed in this study, results in decreased general activity and mobility (Borner et al., 2015; Engström-Öst & Mattila, 2008; Gray et al., 2011; Leahy et al., 2011). In contrast, other species increase their activity, likely to counteract reduced foraging efficiency in turbid waters (Fischer & Frommen, 2013; Sweka & Hartman, 2001; Wishingrad et al., 2015). The reasons for these varied responses remain unclear. A recent meta-analysis indicates that significant differences among species cannot be attributed to factors such as trophic position, size, eye size, turbidity source or ecosystem type (Rodrigues et al., 2023). Instead, additional species-specific traits or local ecosystem factors likely play a role. The fishes' foraging and energy constraints could potentially link to their behavioural responses. These effects may interact in more complex ways with the species' ecological characteristics, which we have not yet identified.

The reduction in territorial defence behaviour and exploration documented in these experiments, as a consequence of increased turbidity, has the potential to affect both the social interactions and feeding ecology of *N. pulcher*. This species is highly social and lives in cooperative, territorial groups and breeds in cavities dug out in the substrate (Balshine-Earn et al., 1998; Jungwirth et al., 2023; M. Taborsky & Limberger, 1981). Groups are part of large colonies that may consist of hundreds of groups, sometimes including other substrate-brooding cichlid species (Jungwirth & Taborsky, 2015; Jungwirth et al., 2023; Taborsky & Limberger, 1981). When feeding, group members leave their territories to feed on floating particles in the water column above them (Gashagaza, 1988). Our results suggest that the behavioural changes elicited by increased turbidity would lead the fish to feed closer to their territories, potentially reducing the effectiveness of foraging (Heg & Taborsky, 2010). These modifications could result in reduced growth rates and potentially decreased survival rates. Previous research has also suggested that when *N. pulcher* spends more time in and close to the shelter, aggression rates between group members may increase (Heg & Taborsky, 2010). In contrast, aggression towards territorial neighbours may decrease because of increased turbidity, as suggested by our results. Investigating how the net changes in intraspecific aggression affect the growth and survival of cichlids in turbid conditions would be a critical step towards a more complete assessment of the effects of turbidity on the Lake Tanganyika fish population.

We investigated the behavioural responses of *N. pulcher* to a short-term increase in sediment-induced turbidity, followed by a gradual decrease as the sediment settled. We simulated the effects of abrupt river runoff from landscapes with land uses that elevate erosion processes. However, because of the ongoing issue of eutrophication in Lake Tanganyika (Moshi et al., 2022; Shen et al., 2022; Yu et al., 2018), we are likely to observe prolonged periods of increased turbidity caused by phytoplankton blooms. It remains unknown whether *N. pulcher* would habituate to higher turbidity if the changes in turbidity were long-lasting, whether the behavioural changes that we saw in our experiments would persist long-term or what potential developmental effects there may be (Gray et al., 2012). It is also unclear whether and how the behavioural changes to turbidity may impact the viability of this and other social Tanganyikan fish species, which rely on visual displays for communication and visual predator detection. Future research should investigate the processes by which fish adjust to long-term increases in turbidity, as well as the impact of turbidity on group behaviours, such as interactions between breeding fish and their helpers, territory size, feeding rates and vulnerability to predators. Understanding these factors would provide critical information about how a turbid environment affects *N. pulcher* and the wider variety of cichlids in Lake Tanganyika.

## Author Contributions

**Markus Zöttl:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Jessica Cuccuru:** Writing – review & editing, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Adrian Berge:** Writing – review & editing, Conceptualization. **Kristofer Bergström:** Writing – review & editing, Conceptualization. **Henrik Flink:** Writing – review & editing, Conceptualization. **Marc M. Hauber:** Writing – review & editing, Visualization, Conceptualization. **Samuel Hylander:** Writing – review & editing, Conceptualization. **Francesca Leggieri:** Writing – review & editing, Conceptualization. **Oscar Nordahl:** Writing – review & editing, Conceptualization. **P. Andreas Svensson:** Writing – review & editing, Conceptualization. **Petter Tibblin:** Writing – review & editing, Resources, Funding acquisition, Conceptualization. **Carl Tamario:** Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization.

## Data Availability

The code and data to reproduce the analyses and figures are available at https://doi.org/10.6084/m9.figshare.27935643.v1. See Zöttl et al. (2025).

## Declaration of Interest

The authors declare no competing interests.

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## Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123243.

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