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# Investigating Trait-Based Capture Vulnerability and the Potential for Selection in the Amazonian Ornamental Fishing Industry

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# Abstract

The harvest of animals from the wild is a pervasive selective force, especially in fisheries, where harvesting often targets individuals with specific traits. Early research on trait-based selection was particularly focussed on traits related to age and size at maturation, but there has been a more recent shift toward understanding how traits beyond growth, such as behavioural and physiological traits, may also be targets of selection. Indeed, there is now emerging evidence from commercial and recreational fisheries that individuals with physiological traits related to metabolism and swimming performance are more likely to be captured, as are fish with behavioural traits related to exploration, risk-taking, and group cohesion. However, the direction of selection has been found to be largely dependent on the type of gear used, with more active gears such as trawls targeting traits relating to swimming capacity, and more passive gears such as traps targeting traits related to increased risk-taking and exploratory behaviour. Many of the traits under selection are also influenced by environmental factors such as temperature and oxygen availability, but how environmental factors modulate capture vulnerability is currently not well understood. Another important gap in fisheries selection literature is that some fishery sectors have been completely overlooked including smaller-scale artisanal fisheries such as the ornamental trade, a global industry with important repercussions for sustainability, biodiversity, and the livelihoods of local communities.

In this thesis, for the first time, I aimed to uncover if there was a potential for trait-based selection in the ornamental fishing industry, specifically in the Amazon, which is home to a large proportion of wild-caught ornamental species. Using a combination of lab-based studies and field observations, I investigated capture vulnerability and compared phenotypes of key ornamental species caught using different gears. I also examined the impact of environmental factors on behavioural and physiological traits to determine if the environment can modulate relationships between individual phenotype and capture vulnerability.

Chapter 1 introduced the main research themes and highlighted the key knowledge gaps that were addressed in this thesis. In chapter 2, I used a scaled-down fisheries simulation that has been used in previous studies focussed on commercial and recreational fisheries. Unlike previous studies, which have used surrogate species, I used an actual target species of the trade, the cardinal tetra (*Paracheirodon axelrodi*), which is a highly popular ornamental species. I repeatedly caught individuals to determine their vulnerability to capture and tested whether vulnerability to capture can be predicted by phenotype. I revealed that capture

vulnerability is predicted by a suite of traits, namely size, swimming endurance, exploration, and risk-taking.

In chapter 3, I caught wild populations of cardinal tetra using active (net) and passive (trap) gear types and examined differences in behavioural and physiological traits in the lab. I used a range of assays including constant acceleration tests, maze tests, open field, and novel object tests. Trap-caught fish were larger and had a lower swimming performance compared to net-caught fish. In contrast, net-caught fish were more cohesive and active, but specific results varied across assays. Social and environmental factors also influenced findings, with differences in risk-taking revealed between individuals and groups and even small variations in ambient temperature during trials significantly influencing behaviour.

In chapter 4, I used a completely field-based approach to investigate the ornamental capture process *in-situ*. Using underwater recording of traps in the Amazon, I observed behaviours for two species, the spotted tetra (*Copella nattereri*) and *Hemigrammus Spp.,* including pre-capture behaviours such as passes and inspections, which have not been observed in the majority of fisheries selection studies. The observations revealed that the majority of fish that inspected traps did not enter them, and while the likelihood of capture was similar for both species, once a given trap had caught one species, it would not catch the other. There were also differences between species in the frequency and timing of behaviours, such as passes and inspections. There was also a relationship between environmental factors and behaviours, but these differed between species, highlighting the importance of integrating multiple species in studies.

In chapter 5, I captured spotted tetra using active (net) and passive (trap) gears and examined behavioural traits of groups using open field and novel object tests after a short acclimation time. I also investigated the impact of an acute temperature increase on behavioural traits. I found that trap-caught fish were more exploratory and showed greater group cohesion, while net-caught fish were more active. Interestingly, there was limited evidence that exposure to an elevated temperature influenced any behavioural traits apart from cohesion. However, group identity accounted for a large amount of behavioural variation, as individual responses were masked at the group level, highlighting an important dynamic to consider when interpreting the potential for selection.

Finally, in chapter 6, I summarised the key findings and overarching themes of my thesis. I discussed the potential for selection in the ornamental fishing industry and highlighted how my findings contribute to the existing body of literature. I then provided an overview of the challenges and limitations of my thesis and provided some future directions for the field.

Taken together, my thesis provides an important foundation towards understanding the potential for selection in ornamental fisheries. Using lab simulations and field observations across different environmental contexts, this thesis shows that capture is not random, but trait based. This thesis also highlights the potential for gear-based selectivity in the ornamental fishing trade, which can have important repercussions for biodiversity and conservation. This thesis also raises questions about how selection operates in different environmental conditions or how group dynamics can mask individual responses. In summary, this thesis contributes a novel perspective on fisheries-induced selection by focusing on a previously overlooked system and broadens our understanding of how artisanal fisheries can shape wild populations.

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# Declaration of Authorship

I declare that this thesis is the result of my own work, except where explicit reference is made to the work of others. This thesis has not been presented in any previous application for a degree at this or any other institution.

Signature:

Printed Name: Mar Deniz Yerli Pineda

# Co-authorship Statement

Chapter two author contributions: Mar Pineda designed and conceived the study, with assistance from Daiani Kochhann and Shaun S. Killen. Data were collected by Mar Pineda, with assistance from Daiani Kochhann, Belle Valiulis and Nicola Herlihy. Videos were analysed by Mar Pineda. Statistical analyses were carried out by Mar Pineda. Mar Pineda wrote the paper. All supervisors gave feedback on the final draft of the paper.

Chapter three author contributions Mar Pineda designed and conceived the study, with assistance from Daiani Kochhann and Shaun S. Killen. Fieldwork was carried out by Mar Pineda, Daiani Kochhann, and Valderiz Soares Siqueira. Data were collected by Mar Pineda with assistance from Daiani Kochhann. Video data were analysed by Mar Pineda. Statistical analyses were carried out by Mar Pineda. Mar Pineda wrote the paper. All supervisors gave feedback on the final draft of the paper.

Chapter four author contributions Mar Pineda designed and conceived the study, with assistance from Daiani Kochhann and Shaun S. Killen. Fieldwork was carried out by Mar Pineda, Daiani Kochhann, Shaun S. Killen, and Jose Lindoso Garrido Melo. Video data were collected and analysed by Mar Pineda. Statistical analyses were carried out by Mar Pineda. Mar Pineda wrote the first draft of paper. Funding was generated by Mar Pineda, Shaun S. Killen, Daiani Kochhann, and Adalberto L. Val. All supervisors gave feedback on the final draft of the paper. A version of this paper was published in the Journal of Fish Biology: Pineda, M., Kochhann, D., Garrido Melo, J. L., Lindström, J., Elmer, K. R., Val, A. L., & Killen, S. S. (2025). Species-specific behaviour and environmental drivers of trap interactions in wild ornamental fishes. *Journal of Fish Biology*, 1–14. **https://doi.org/10.1111/jfb.70217**

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# List of Abbreviations

AIC – Akaike Information Criteria

AND – Average Neighbour Distance

BL/S – Body Lengths Per Second

C – Caught

CAT – Constant Acceleration Test

CC – Caught Twice

CCC – Caught Three Times

CD – Coefficient of Dispersion

E – Escaped

EE – Escaped Twice

EEE – Escaped Three times

FIE – Fisheries Induced Evolution

GLM – Generalised Linear Model

INPA – National Institute for Amazonian Research

IUCN – International Union for Conservation of Nature

NO – Novel Object

PC – Principal Component

PCA – Principal Component Analysis

SD – Standard Deviation

SDR – Sustainable Development Reserve

SL – Standard Length

TL – Total Length

UV – Ultraviolet

# Chapter 1

# General Introduction

## 1.1 Human-Induced Selection

Understanding the impact of human activity on natural populations has become an increasingly important theme in biological literature. Human-mediated selection in particular, is one of the most pervasive selective forces on Earth (Baltazar-Soares et al., 2021; Hendry et al., 2017; Palkovacs et al., 2012). Since the dawn of humanity, our actions have altered the phenotypic composition of wild populations across terrestrial (Coltman et al., 2003; Pigeon et al., 2016; Pilot et al., 2021; Van De Walle et al., 2021), freshwater (Candolin and Jensen, 2021; Cooke et al., 2007; Crotti et al., 2021; Redpath et al., 2010), and marine ecosystems (Hočevar and Kuparinen, 2021; Hutchings and Kuparinen, 2020). The drivers of phenotypic change are numerous, and well-documented in the literature (reviewed by Baltazar-Soares et al., 2021 and Palkovacs et al., 2012), including agriculture and domestication (Alexandre et al., 2025; Pilot et al., 2021; Varah et al., 2019), habitat modification (Bettencourt-Amarante et al., 2025; Desrochers, 2010; Wild and Gienger, 2018), climate change and pollution (Blechschmidt et al., 2020; Jones et al., 2023; Zimova et al., 2016), and harvesting (Enberg et al., 2012; Pigeon et al., 2016; Van De Walle et al., 2021). See Figure 1.1 for case studies.

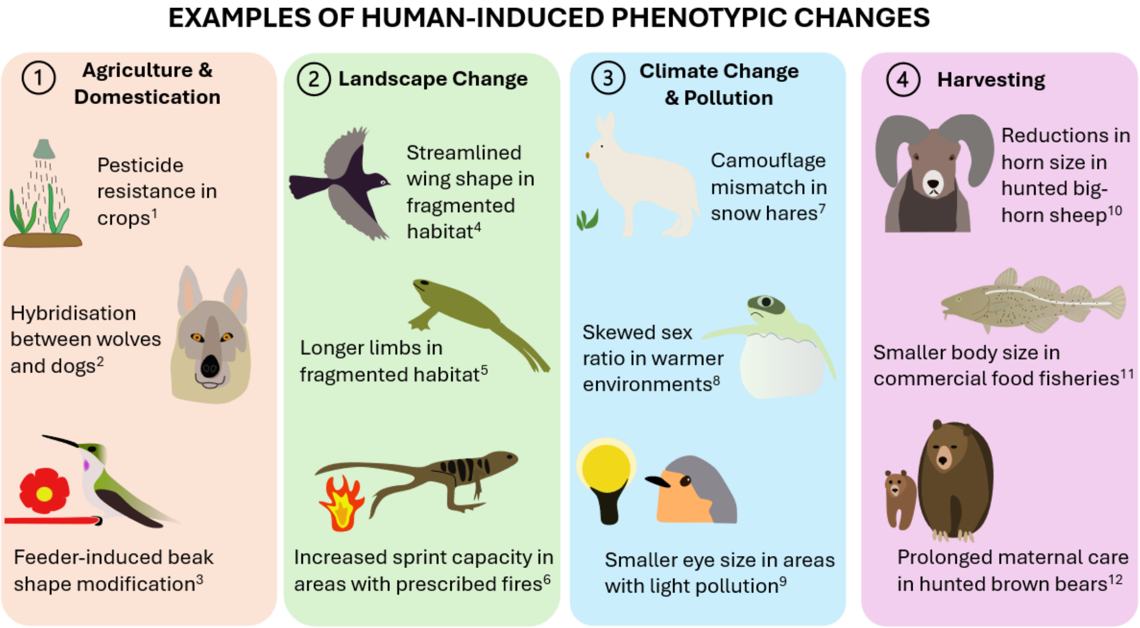

**Figure 1.1)** Sources of human-induced phenotypic changes in wild populations, characterised under four categories: 1) agriculture and domestication-[1] (Varah et al., 2019), [2] (Pilot et al., 2021), [3] (Alexandre et al., 2025) ; 2) landscape change - [4] (Desrochers, 2010), [5] (Bettencourt-Amarante et

al., 2025), [6] (Wild and Gienger, 2018) ; 3) climate change and pollution- [7] (Zimova et al., 2016), [8] (Blechschmidt et al., 2020), [9] (Jones et al., 2023); and 4) harvesting- [10] (Pigeon et al., 2016), [11] (Enberg et al., 2012), [12] (Van De Walle et al., 2021).

While the outcomes of human activities are well documented, the mechanisms by which phenotypic change occur are less well understood. Phenotypic changes can arise via phenotypic plasticity, where individuals respond to environmental changes without genetic shift (Dupont et al., 2024), or via evolution, which requires the presence of selective pressures acting on variable and heritable traits (Law, 2000). Phenotypic changes can also arise through a combination of both phenotypic plasticity and evolution (Hendry et al., 2011), and disentangling these mechanisms remains a key challenge (Hendry et al., 2017). Nevertheless, there is mounting evidence that both can contribute meaningfully to rapid trait changes under anthropogenic pressure (Hendry et al., 2011) and that phenotypic changes can have far-reaching ecological consequences. From feedback into ecological dynamics (Fussmann et al., 2007; Kinnison and Hairston, 2007), altering species interactions (Agrawal et al., 2006), and population resilience (Bijlsma and Loeschcke, 2012), it is clear that understanding human-induced selection is key.

## 1.2 Fishing-Induced Selection

Among all the anthropogenic activities contributing to selection, the intensive harvest of commercial fisheries has received by far the most attention (Enberg et al., 2009; Heino et al., 2015; Hollins et al., 2018a; Hutchings and Kuparinen, 2020; Law, 2000). Perhaps, this is due to the highly non-random nature of fishing, which makes it a striking example of ‘unnatural selection’ (Allendorf and Hard, 2009). Unlike agriculture and aquaculture, where animals have been selectively bred to increase the frequency of desirable traits, the capture of fishes from the wild typically removes the most desirable individuals, increasing the frequency of less desirable phenotypes (Allendorf and Hard, 2009). Indeed, there is now growing evidence that the capture of wild fishes is not only selective, but it can change the evolutionary trajectory of exploited populations (Enberg et al., 2012; Hollins et al., 2018; Jørgensen et al., 2007).

The selective pressures imposed by fishing can have profound consequences for wild fish populations. Fishing often elevates adult mortality, selecting for individuals that mature and reproduce at earlier ages (Heino et al., 2015, 2013; Laugen et al., 2014). Moreover, most fisheries preferentially target larger individuals, exacerbating selection against large body size and for traits that allow earlier reproduction (Sharpe and Hendry, 2009). If the traits under selection are heritable, repeated selection through harvesting can lead to a phenomenon known as fisheries-induced evolution (FIE) (Heino et al., 2015, 2013; Hollins et al., 2018a). Early research into FIE was predominantly focused on traits related to body size, growth, and life history (Enberg et al., 2012, 2009; Law, 2000; Uusi-Heikkilä et al., 2015). However, there is now increasing interest in understanding how other traits, including behavioural and physiological ones, may also be shaped by fishing pressure (Diaz Pauli and Sih, 2017; Hollins et al., 2018a; Monk et al., 2021). These traits can not only be indirectly targeted by fisheries, but variation and heritability in the traits under selection also have the potential to lead to FIE (Crespel et al., 2021a; Hollins et al., 2018a) . Despite this, there has been a paucity of empirical studies demonstrating how selection on physiological and behavioural traits can occur, particularly in wild populations (Hollins et al., 2018a).

## 1.3 Traits Related to Capture Vulnerability

Central to understanding trait-based selection, is uncovering whether particular traits render individuals more vulnerable to capture, which can vary according to the type of fishing gears used (Álvarez-Quintero et al., 2021; Diaz Pauli et al., 2015; Sun et al., 2022). Fishing gears align across a continuum of activity, ranging from active gears such as trawls and purse seines, which directly pursue or encircle fish, and more passive gears such as traps and static hook and line angling, which rely on individuals approaching and voluntarily interacting with a gear (Hollins et al., 2018a). A number of behavioural traits have been linked to vulnerability to capture, including activity level (Koeck et al., 2019), sociability and group cohesion (Álvarez-Quintero et al., 2021; Kressler et al., 2021; Thambithurai et al., 2018), and willingness to take risks (Andersen et al., 2018; Arlinghaus et al., 2017; Klefoth et al., 2017; Monk et al., 2021), which is often described as boldness, although the exact definition varies across studies (Beckmann and Biro, 2013; Réale et al., 2007). Morphological traits such as body mass and physiological traits such as metabolic rate, anaerobic capacity, and swimming performance are also believed to strongly influence interactions with different types of fishing gear (Diaz Pauli and Sih, 2017).

Variation in locomotor and behavioural performance plays a key role in determining capture vulnerability under active fishing gears, which can therefore act as selective agents on these traits. Active gears, such as trawls, are believed to impose selection on locomotor capacity and burst swimming performance, as fish must escape the gear to avoid capture (Killen and Koeck, 2023). While this can be difficult to test using the large-bodied targets of commercial food fisheries, such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), scaled-down laboratory-based fisheries simulations have emerged as useful tools for testing the relationships between phenotypic traits and capture vulnerability

(Crespel et al., 2021a; Thambithurai et al., 2018). For example, using a scaled-down trawl, a positive correlation has been found between anaerobic burst capacity and escape success using the common minnow (*Phoxinus phoxinus*) as a model species (Killen et al., 2015). More recent studies using the same system have also revealed relationships between anaerobic performance and capture outcome, although these vary according to social conditions such as shoal familiarity (Hollins et al., 2019). While less studied, behavioural responses to active gears may also influence vulnerability if more active individuals have better escape capabilities (Álvarez-Quintero et al., 2021; Winger et al., 2016). Sociability and group cohesion have also been linked to capture outcomes. For example, more social fish or those exhibiting stronger group cohesion may be more conspicuous to fishers and thus more susceptible to capture (Guerra et al., 2020). Conversely, fish in larger groups may be better able to avoid capture due to increased information sharing among shoal mates (Brown and Warburton, 1999; Thambithurai et al., 2018).

In contrast, passive gears have received more research attention in the context of selectivity. Physiological traits such as foraging drive and metabolism have been linked with trap entry, although the direction of the effect varies among studies (Thambithurai et al., 2018). Higher metabolism is also associated with boldness and reduced sociability (Killen et al., 2012; McKenzie et al., 2016; Metcalfe et al., 2016), both of which have been repeatedly linked to increased vulnerability of capture from passive gears. A number of studies have found boldness is associated with capture vulnerability, both in lab-based contexts (Álvarez-Quintero et al., 2021), and in semi-natural environments during recreational fishing (Arlinghaus et al., 2017; Cooke et al., 2007; Klefoth et al., 2017). These findings have led to the hypothesis of a "timidity syndrome", where the selective removal of bold individuals may leave behind a more cautious, less responsive population (Arlinghaus et al., 2017; Monk et al., 2021). However, despite an increase in findings that suggest that fishing can drive selection in behavioural and physiological traits, results have often been inconsistent and context-dependent (Hollins et al., 2018), with little consideration for how relationships between individual phenotypes and capture vulnerability can be affected by environment.

## 1.4 The Relationship Between Environment and Capture Vulnerability

Environmental factors can profoundly influence the behavioural and physiological traits of fishes. For example, temperature affects metabolic rate, activity, and boldness (Forsatkar et al., 2016; Killen et al., 2013), while hypoxia reduces locomotor performance (Domenici et al., 2017; Norin and Clark, 2016) and activity (Pineda et al., 2020). Additional environmental variables such as pH have also been shown to widely disrupt behavioural and physiological process (reviewed by Kleinhappel et al., 2019; Sharma, 2019), including foraging behaviour (Lemly and Smith, 1987), predator avoidance (Weiss et al., 2018), and shoal cohesion (Lopes et al., 2016; Nadler et al., 2016). These findings are significant as certain traits could become more or less important for capture vulnerability depending on environmental context (Hollins et al., 2018). Additionally, environmental variation can influence trait variation, repeatability and heritability, all of which are necessary for evolution to occur (Campbell et al., 2017; Hollins et al., 2018a; Melbinger and Vergassola, 2015). It is therefore surprising that few studies have directly explored the role of environmental factors on capture vulnerability. However, recent findings suggest that exposure to acute hypoxia decreases swimming performance and increases vulnerability to capture in a scaled-down trawling simulation (Thambithurai et al., 2019) and that capture vulnerability is influenced by acclimation temperature, but dependent on the type of gear used (Hollins et al., 2021), further highlighting how many findings are context specific.

While the growing body of research on trait-based selection has increased our understanding of capture vulnerability, there is a critical gap in our understanding of human-induced selection. Namely, harvesting for fishes in the wild does not only occur in commercial and recreational fisheries, which to date, have been the only fisheries that have been studied in this context. In contrast, other sectors, including small-scale artisanal fisheries, such as the ornamental trade, have been virtually unexplored, despite the fact that capture is also non-random (Zehev et al., 2015).

## 1.5 The Ornamental Fishing Industry

Artisanal fisheries are typically small scale, community-based operations that play a vital role in supporting food security and local economies across the globe (FAO, 2018, 2016; Júnior et al., 2016). While typically associated with subsistence fishing, artisanal fisheries also involve the capture of live fish for the ornamental trade; a multi-billion-dollar industry (King, 2019), which harvests fish not for consumption, but for behavioural and aesthetic appeal in aquariums (Miller-Morgan, Tim, 2009). Since the 1970s, the demand for ornamental fishes has grown rapidly, with fishkeeping growing by 14% annually (Maceda-Veiga et al., 2016). Today, more than 1 billion fish are traded internationally each year (Evers et al., 2019), although the number is disputed (King, 2019). Around 90% of the total trade volume of ornamental fish is comprised of tropical freshwater species, but the number of species involved varies widely, ranging from 2,000 to 10,000 (Evers et al., 2019; King, 2019; Phang et al., 2019).

Despite difficulties in quantifying the trade of ornamental fish, it is widely recognised that the industry provides an important source of income and employment for local communities in developing countries, particularly in ecologically sensitive areas (King, 2019). One such area is the Amazon Basin. The Amazon Basin boasts over 2,000 species of fish, including endemic and IUCN Red List species (Phang et al., 2019). In the Brazilian Amazon, the municipality of Barcelos in particular has been considered a historic and economic hub for the ornamental fishing trade (Alho et al., 2015; Evers et al., 2019; Fujimoto et al., 2020; Phang et al., 2019; Zehev et al., 2015). Here, the industry has been built around the wild capture of fishes, especially small characins, such as the cardinal tetra (*Paracheirodon axelrodi*), a popular aquarium fish caught in the wild due to difficulty with breeding in captivity (Evers et al., 2019). At the peak of the ornamental trade, the cardinal tetra alone accounted for 70% of total Brazilian fish exports, contributing almost 80% income to the local economy in Barcelos (Zehev et al., 2015), highlighting its economic and cultural significance (Figure 1.2).

**Figure 1.2)** Trade of ornamental fishes in Barcelos. A) Boats carrying ornamental species for export. B) Murals depicting ornamental species. Photos by S.S. Killen and Mar Pineda.

The capture of ornamental species occurs in the dry season and in the Brazilian Amazon, this mainly occurs in the Rio Negro region (Evers et al., 2019; Ferreira and Yamamoto, 2017; Zehev et al., 2015). Here, tributaries narrow into small streams known as *igarapés*, where water levels are low, and fish are more concentrated (Tribuzy-Neto et al., 2021). Fish in the Amazonian ornamental trade are caught by fishers or '*piabeiros*' using active and passive gear types, depending on habitat type and accessibility (da Silva Ladislau et al., 2021; Ladislau et al., 2020). A typical example of an active gear is the *rapiché*, a specialised dip-net used in areas free of vegetation, while the baited trap *cacurí*, is a passive gear used in areas that are harder to access (Prang, 2007), with both gears (Figure 1.3) designed to capture fish without causing damage to the fish.

**Figure 1.3)** Artisanal gears used to capture Amazonian ornamental fish species. A) *cacurí* - a cylindrical trap made of fine mesh with a narrow funnel-shaped opening; B) *rapiché*- a modified hand net. Photos by S.S. Killen.

In addition to the seasonal reductions in water level, ornamental species in the Rio Negro region experience distinct abiotic conditions. The Rio Negro is a blackwater system characterised by low conductivity, low nutrients, and low pH ranging from 3.7 to 5.4 (Johannsson et al., 2026; Val and Almeida-Val, 2012). Ornamental fishes in this region also experience temperatures typically ranging between 24°C in the wet season and 29-31°C in the dry season (Val and Almeida-Val, 2012), with recent heatwave events in 2023 seeing increases of 3.0°C above the long-term average (Espinoza et al., 2024). Consequently, fishes targeted for the ornamental trade, including species such as the cardinal tetra, regularly experience combinations of elevated temperature, low oxygen availability, and acidic conditions. Such environmental conditions are known to influence behavioural and physiological performance, and may therefore influence the distribution of species, potentially shaping how individuals detect and interact with fishing gears.

While the ecological and economic importance of the ornamental fishing trade has been widely recognised, and the gears used in the capture process have been documented, the potential for targeting specific phenotypes remains unknown. This represents a critical gap in our understanding of human-induced selection as the potential for phenotypic change has wide repercussions for sustainability and population resilience in one of the most biodiverse regions of the planet.

## 1.6 The Potential for Fishing-Induced Selection in the Ornamental Fishing Industry

Given the evidence that human activities such as harvesting and fishing can impose selective pressures on wild populations, it is surprising that research on trait-based selection has not investigated the entire range of fishing that exists. As outlined in previous sections, our understanding of fishing-induced selection largely comes from commercial and recreational fisheries, where capture is non-random and harvests individuals with certain morphological, physiological, or behavioural traits, potentially leading to fishing-induced evolution (FIE). However, despite the economic and ecological significance of the ornamental fishing trade, its potential role in driving phenotypic change has received virtually no attention.

This thesis aimed to explore whether harvesting in the ornamental fishing industry, namely in the Amazon, may exert similar trait-based selective pressures. This gap in knowledge is especially notable as piabeiros frequently select fish based on observable traits such as morphology, size, and colouration (OATA, 2016). However, as in other fisheries, it is likely that additional and less observable traits, such as behaviour and physiology, may also be under direct selection.

Fishing gears play an important role in shaping selection in commercial and recreational fisheries. The ornamental trade similarly uses both active and passive gears, and it is possible that these gears may also capture individuals with distinct phenotypes, in a manner analogous to commercial and recreational fisheries (Figure 1.4). For example, active *rapiché* are used to directly pursue and net groups of fish (Prang, 2007). It is therefore possible individuals with greater anaerobic capacity, improved burst swimming performance, or enhanced escape responses may be more likely to evade capture, resulting in selection against those traits over time. Behavioural traits could also be under selection from netting, as more cohesive or social individuals may form tighter shoals and be more easily detected and captured, potentially leading to reduced sociability in future generations if the traits are heritable. On the other hand, as the passive *cacurí* trap relies on voluntary entry and is often baited to attract fish, traits such as higher metabolic demand and foraging drive as well as risk-taking and exploratory behaviours may increase vulnerability to these gears (Figure 1.4). Over time, this could lead to selection against risk-taking, activity, and exploration, reinforcing patterns observed in other passive gear studies and contributing to the hypothesised "timidity syndrome" (Arlinghaus et al., 2017).

As outlined in section 1.4, environmental variables such as temperature, oxygen availability, and pH strongly influence the expression of behavioural and physiological traits relevant to capture vulnerability. Furthermore, as outlined in section 1.5, in tropical regions like the Amazon, elevated temperatures, hypoxia, and low pH are common and can fluctuate dramatically seasonally and daily (Val and De Almeida-Val, 1995). As such, ornamental species may already be living close to their upper physiological limits (Campos et al., 2019), making them sensitive to environmental stressors, and modulating relationships between trait expression and vulnerability to capture. For example, hypoxia may limit locomotor performance, rendering individuals more vulnerable to netting. Similarly, elevated temperatures may increase metabolic rates, potentially amplifying the influence of risk-taking behaviour on trap entry.

The characteristics of ornamental species also highlight they are ideal candidates for investigating fisheries-induced selection. Many targeted ornamental species are small bodied with rapid generation times, making potential evolutionary consequences detectable over shorter time periods. Their widespread use in aquaria also highlights their suitability for holding and testing fish in controlled laboratory settings. Ornamental species therefore provide an ideal opportunity to investigate fisheries selection using the actual target species of capture rather than relying on surrogate species such as zebrafish or minnows, which may not always directly relate to the larger-bodied species they are attempting to replicate (Killen and Koeck, 2023). Additionally, their small size and abundance in natural environments also allows researchers to reliably observe their behaviour *in-situ*, making them ideal candidates for combined lab and field studies, which allow researchers to explore mechanisms behind capture in ecologically realistic scenarios (Binning et al., 2025).

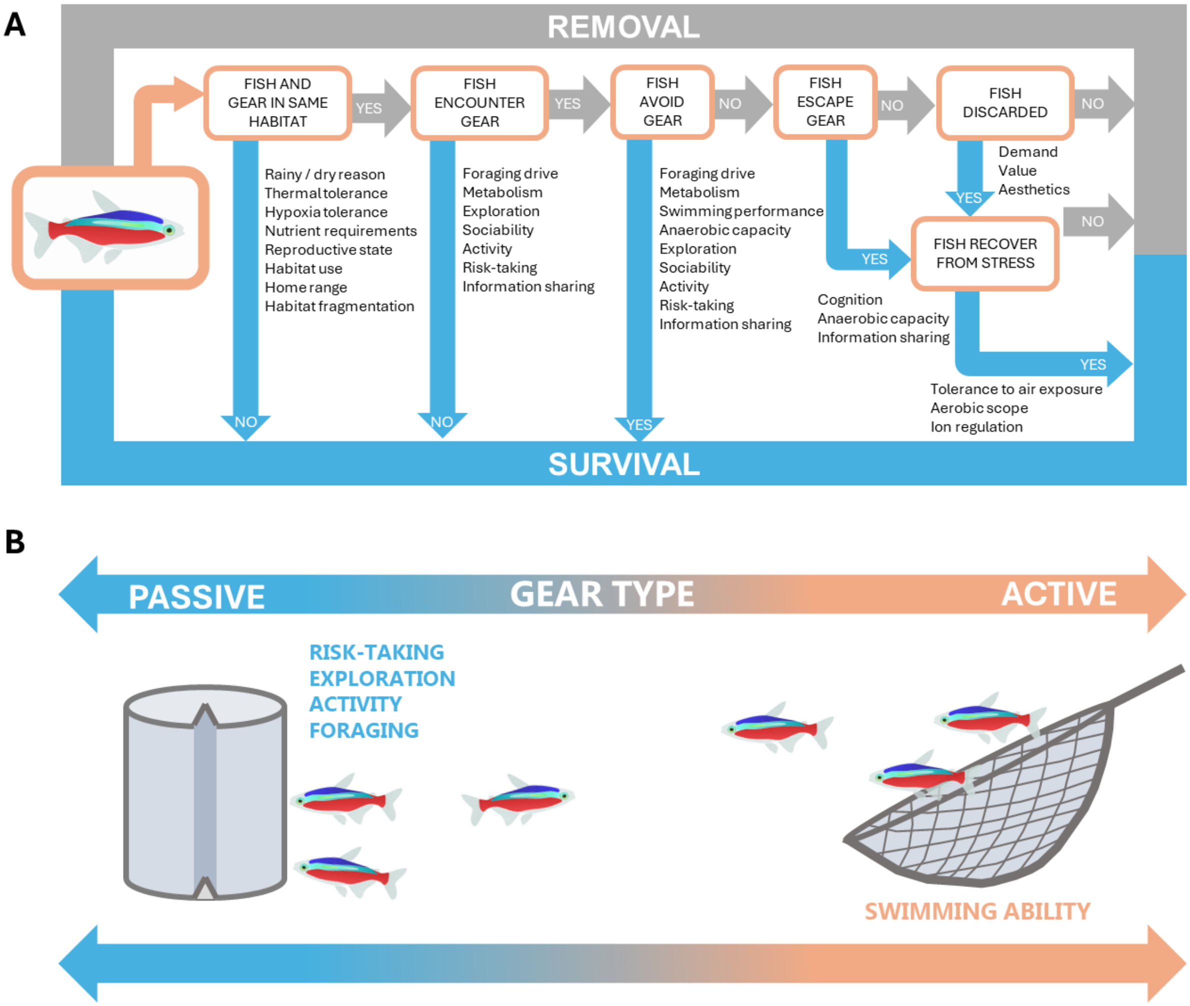

**Figure 1.4)** Schematic demonstrating the potential for fishing-induced selection in the ornamental fishing trade. A) Possible traits and factors involved in determining survival outcomes, with factors in one step influencing the next. Adapted from Killen and Koeck (2023). B) Potential traits captured by active and passive artisanal gear types. Adapted from Hollins et al (2018).

## 1.7 Thesis Aims

In this thesis, I aimed to uncover for the first time, if there is a potential for selection in the ornamental fishing industry. In Chapter 2, I used a lab-based, scaled-down trapping simulation to explore whether wild-caught cardinal tetra differ in vulnerability to capture, and if vulnerability to capture is influenced by behavioural and physiological traits. In Chapter 3, I explored if cardinal tetra caught using traditional artisanal active and passive gears differ in their behavioural and physiological traits. In Chapter 4, I used an entirely field-based approach and analysed underwater videos of *cacurí* to explore the capture process in more detail, including pre-capture behaviours of multiple ornamental species. I also explored the relationships between observed behaviours and naturally occurring environmental variables such as temperature, oxygen saturation, and pH. In Chapter 5, I compared the behavioural traits of spotted tetra caught using active and passive gears. I also explored whether the behaviours of net-caught and trap-caught fish are influenced by an acute increase in temperature. Finally, Chapter 6 presented a general discussion of the findings of my thesis, along with implications and future directions.

# Chapter 2

# Boldness, exploration, and endurance influences vulnerability to capture in the cardinal tetra, *Paracheirodon axelrodi*

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## 2.1 ABSTRACT

Intense fishing represents one of the strongest selective anthropogenic pressures exerted on natural populations. In commercial food fisheries, there is increasing evidence that physiological and behavioural traits can be associated with vulnerability to capture by fishing gears. However, the selective impact of fishing has been overlooked within the context of the ornamental fishing industry. Here, I examine the relationship between individual phenotype and vulnerability to capture in the cardinal tetra (*Paracheirodon axelrodi)*, a popular aquarium species. Using a lab-based simulation with an artisanal trap, individuals (n = 500) were repeatedly caught to determine vulnerability to capture. Behavioural assays were then carried out on high and low vulnerability individuals to determine sociability, exploration, activity, and boldness. Body mass and time until fatigue were also examined for each individual and linked to capture vulnerability. I found that bolder, more exploratory, and active individuals were more vulnerable to capture, as were fish that were smaller and fatigued faster, while sociability and activity had no relationship with capture vulnerability. The percentage of captured individuals declined over successive fishing rounds, suggesting the potential for learning or gear avoidance. This is the first empirical study demonstrating that behavioural and physiological traits are directly linked to capture vulnerability in an ornamental species, offering an initial step toward understanding how trait-based selection can operate in this understudied fishery.

## 2.2 INTRODUCTION

The harvest of animals from the wild can be both intensive and selective (Baltazar-Soares et al., 2021). In fish populations, harvesting not only depletes stocks but can also influence the evolutionary trajectory of a population (Enberg et al., 2012). Research has indicated that over time, fishing has resulted in changes to life history traits such as growth rate, size at maturity, and reproductive success (Bowles et al., 2020; Ernande et al., 2004; Heino et al., 2015; Young et al., 2020). When these traits are heritable, this can lead to a phenomenon known as fisheries-induced evolution (FIE) (Heino et al., 2015; Jørgensen et al., 2007; Law, 2000; Uusi-Heikkilä et al., 2015). While FIE research has typically focussed on life-history traits, growing evidence suggests that behavioural traits such as boldness, activity level, and sociability can also influence an individual's vulnerability to capture (Crespel et al., 2021a; Diaz Pauli and Sih, 2017; Hollins et al., 2018a; Koeck et al., 2019).

Determining which traits render individuals more susceptible to capture is crucial for understanding FIE and is dependent on the type of gear used (Hollins et al., 2018a; Sun et al., 2022). For example, active gear types such as trawls, pursue prey and capture individuals as they fall back into the oncoming net, and may be more likely to target individuals with poorer swimming performance (Arlinghaus et al., 2017; Biro and Dingemanse, 2008; Killen et al., 2015). Conversely, passive gear types, such as baited traps, do not actively chase or encircle prey, but instead rely on individuals encountering and voluntarily entering a gear. Behavioural traits such as exploration, boldness and sociability have been linked to an individual's capture vulnerability (Arlinghaus et al., 2017; Diaz Pauli et al., 2015; Kressler et al., 2021; Monk et al., 2021). Bolder individuals have a higher risk-taking tendency, and as such, are more likely to approach unfamiliar or novel objects (Andersen et al., 2018; Klefoth et al., 2017). Similarly, exploratory fish may be more likely to encounter a trap (Hollins et al., 2018a), and individuals that are more social may be more likely to follow others into a trap (Thambithurai et al., 2018). Additionally, morphological traits such as body mass and physiological traits such as swimming endurance may influence an individual's ability to escape a gear (Hollins et al., 2018a). While endurance is a performance trait that is particularly useful to understand escape from active gears, it may also reflect underlying physiology capacity or condition that can influence broader behavioural traits such as activity or exploration, which can affect vulnerability to passive gears.

Despite increasing attention to the role of behavioural traits in capture vulnerability (Álvarez-Quintero et al., 2021; Diaz Pauli and Sih, 2017; Leclerc et al., 2017), most mechanistic research has relied on using surrogate species in controlled laboratory settings to extrapolate findings to commercial food fisheries (Crespel et al., 2021a; Hollins et al., 2019; Thambithurai et al., 2018). Lab-based simulations, which replicate the final moments of capture, are often used as a tool to understand how individual traits can influence susceptibility to capture. However, relating these lab-based scenarios to actual fisheries can be challenging, particularly when the surrogate species differ in behavioural and physiological traits compared to the actual target species (Killen and Koeck, 2023). Moreover, to date, research in fishing-induced selection has only focused on commercial and recreational fisheries, with entire fishing sectors completely overlooked, including smaller scale artisanal fisheries such as the ornamental fishing trade.

The ornamental fishing trade is a global multi-billion-dollar industry (King, 2019) with important consequences for conservation and sustainable development (Evers et al., 2019; Maceda-Veiga et al., 2016; Phang et al., 2019). While the trade has become increasingly popular, both in terms of consumer demand (King, 2019; Maceda-Veiga et al., 2016), and in research focus (Peh and Azra, 2025), very little is known about the ecological and evolutionary consequences of capturing fish for the trade (Ojelade et al., 2024). This is surprising, not only due to economic and ecological repercussions, but because they provide a useful opportunity for investigating fisheries selection in a relevant target species. Ornamental fishers often target specific species, and among these, particular traits are targeted, such as certain sizes and colourations. Ornamental species are also targeted using both active and passive gear types. Therefore, there is a potential for selective pressures to operate in a manner analogous to commercial food fisheries. Moreover, as ornamental species are smaller-bodied and easier to study in the lab, they are ideal candidates for lab-based simulations, particularly for ornamental species that are harvested from the wild.

The cardinal tetra (*Paracheirodon axelrodi*) is a popular aquarium species that is typically wild-caught due to difficulties with captive breeding (Ladislau et al., 2020). Historically, the trade of cardinal tetra has dominated within the Amazon Basin (Evers et al., 2019; Tribuzy-Neto et al., 2021; Zehev et al., 2015). Here, individuals are caught using modified handheld nets, an active gear known as *rapiché*, as well as the more passive *cacurí*, which is a trap typically baited with fish or manioc powder (Prang, 2007). However, it is currently not known whether cardinal tetras differ in their vulnerability to capture, and whether individual traits influence capture vulnerability as they do in commercial food fisheries. Cardinal tetra display a wide range of behaviours that could be associated with an increased vulnerability of capture. In the wild, cardinal tetra are highly social (Cavallino et al., 2023), forming large shoals (Stevens et al., 2022). While shoaling behaviour likely plays an important antipredator role, it may also serve to increase likelihood of capture as social individuals may be more likely to follow others into traps (Álvarez-Quintero et al., 2021) and larger groups may also be more conspicuous to fishers (Guerra et al., 2020). The foraging ecology of cardinal tetra may further influence capture vulnerability. In the wild, cardinal tetra forage in slow-moving shallow waters and feed on small invertebrates in submerged vegetation and leaf litter (Walker, 2004). Such reliance on active foraging suggests that exploratory behaviour could be selected on if exploratory individuals are more likely to encounter and enter fishing gears.

While the dynamics of ornamental fish capture remain poorly understood, experimental lab-based approaches provide the control necessary to disentangle the behavioural and physiological factors influencing vulnerability to capture. In this study, I investigated the potential for passive artisanal gears to select on behavioural and physiological traits. Specifically, I aimed to address the following questions: 1) How do individuals differ in their vulnerability to capture; 2) is vulnerability to capture associated with behavioural and physiological traits? I hypothesised that cardinal tetra would differ in capture vulnerability and that specific behavioural traits such as boldness and exploration, and physiological traits such as swimming performance, would be linked to a higher vulnerability of capture.

## 2.3 METHODS

### 2.3.1 Study Species

Juvenile cardinal tetras (*Paracheirodon axelrodi*) were obtained from a specialist ornamental fish supplier (TropCo, Tonbridge, UK) (n = 500) and transferred to University of Glasgow aquaria and maintained in two 300 L glass stock tanks. Cardinal tetra were wild caught from the Amazon although their exact origin is unknown. Stock tanks were supplied with recirculating, UV-treated freshwater at 28°C under a 12 h light:12 h dark photoperiod, and equipped with shelter, plastic plants, and a sandy substrate. All fish were acclimated to these conditions for two months. Fish were fed twice daily with commercial feed (TetraMin 115) and were fasted 24 h before experiments. Water quality parameters (pH, ammonia, nitrate, nitrite) were monitored throughout the study and tested weekly. All experiments in this study were performed under UK Home Office Project License (no. 60/4461). and approved by the University of Glasgow Research Ethics Committee. All applicable international, national, and institutional guidelines for the use of animals were followed.

### 2.3.2 Vulnerability Assays

Vulnerability to capture was determined by trapping individuals with a custom-built artisanal trap. Trapping trials were conducted in a fibreglass tank (1 x 1 m), filled to a depth of 26 cm with temperature-controlled water (28 ± 0.3°C mean ± SD). The fibreglass tank was left bare and seven artificial plants were used to provide shelter. A weighted column (25 x 20 cm) made of a thick plastic mesh was placed in the corner of the tank and used as an acclimation zone for fish prior to the start of each trial and was equipped with a pulley system to release fish at the start of the trial. A custom-built *cacurí* was used for trapping. The trap was a cylindrical (45 x 23 cm) steel frame covered in white netting (<1.5 mm mesh size) with an inverted funnel entrance measuring ~2 cm across (Figure 2.1). Traps were not baited at any point during trials. The location of the acclimation zone, traps, and plants were kept consistent across trials. A dark curtain was placed around the perimeter of the tank to minimise external disturbance. A video camera (GoProHero 7) was attached to a frame above the arena and set to 60 frames per second.

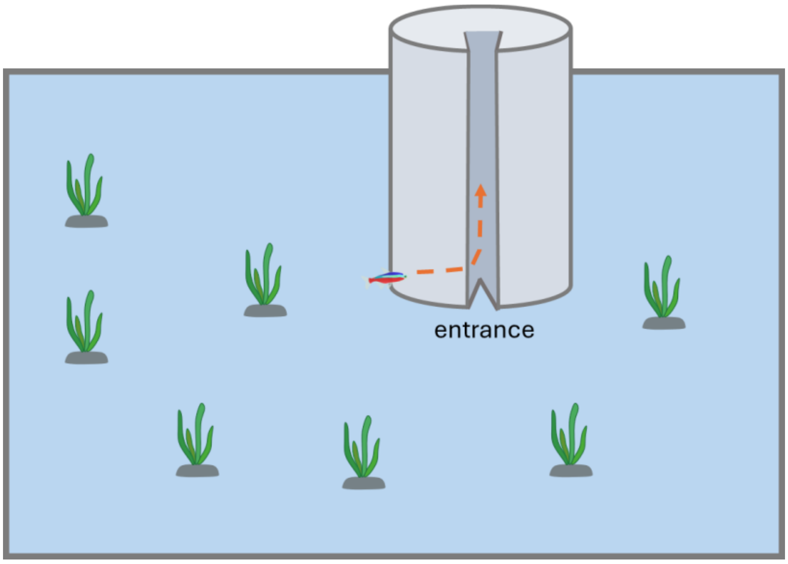

**Figure 2.1)** Schematic of apparatus used in vulnerability assays (not to scale). Assays were conducted within a fibreglass tank with a custom-built trap and artificial plants. The trap was comprised of a cylindrical steel frame covered in mesh netting, with a funnel-shaped entrance along the front of the trap. The entrance is shown in a darker grey colour and an example is shown of how a fish can enter the trap.

Three successive trapping trials (fishing rounds) were carried out over the course of the study. During the initial fishing round, a group of 40 fish were randomly netted from the same stock tank and then transferred to the acclimation zone within the experimental tank. To obtain accurate video measures of each trial and to minimise further disturbance, recordings were started when fish were placed into the acclimation zone. Following a five-minute acclimation period, the pulley system was used to release fish during the trial. Fish were then allowed to move freely as a group and enter the trap. The trial was stopped when roughly half of the fish had entered the trap. As fish tended to enter in groups and in succession, the trial was stopped when there was a natural division between individuals that approached and entered the trap and those that avoided the trap. No fixed maximum duration was imposed. This resulted in numbers of captured individuals that did vary, as well as a difference in trial durations, ranging from 16-570s (mean ± SD: 168.9 ± 138.264s). The time taken in seconds for the first fish to enter a trap was observed for each trapping trial and was described as entry latency. At the end of a fishing trial, fish that had been captured were immediately separated from the rest of the group by blocking the trap from further entry or exit to allow for accurate counting of fish. This was used to calculate the percentage of fish caught during each trial. After the fishing round, fish were then housed in separate tanks according to whether they had been caught during the trial (C) or escaped the trap (E). This first round of fishing was carried out in the same manner until all 500 individuals had been tested.

After one week, a second round of fishing was carried out on individuals from the C and E category. The same method was used in the second round of fishing, with individuals again separated at the end of the trial according to whether they had been caught or escaped. At the end of the second round, fish had either been caught twice (CC), escaped twice (EE) or a mixture of the two (CE, EC). Following another one week acclimation period, a third and final fishing round was done on the most extreme vulnerability categories (CC and EE), resulting in fish that had either been caught repeatedly (CCC) so were considered most vulnerable, or escaped repeatedly (EEE) so were considered least vulnerable, or varied in vulnerability to different degrees (CCE, EEC) (Figure 2.2). Fish from the high and low vulnerability groups were then used in the behavioural and physiological experiments.

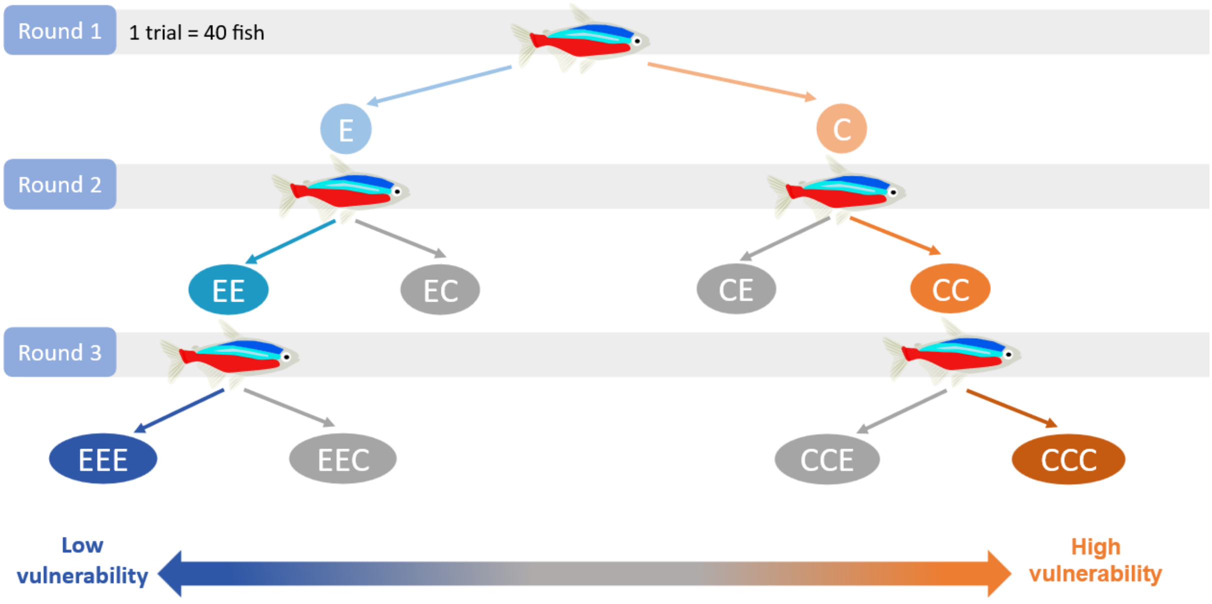

**Figure 2.2)** Method for simulated fishing protocol. Three rounds of fishing were done on 500 cardinal tetras. In the first round, fish were either caught (C) or escaped (E). In the second round, fish from the caught round (C) were trialled again and were either caught again (CC) or escaped (CE). Fish from the escaped round (E) were trialled again and either escaped for a second time (EE) or were caught the second time (EC). The most extreme categories were then trialled again in a third round of fishing. After the third round, fish had been caught three times (CCC), escaped three times (EEE), or a mixture of caught and escaped (CCE and EEC). This was used to determine the fish most and least vulnerable to capture.

### 2.3.3 Behavioural Traits: Set-Up

Following trapping trials, sociability tests were run on focal individuals with high and low capture vulnerability phenotypes. Sociability tests were carried out in a glass tank (77 x 56 x 20 cm, water depth 6 cm) held within an aerated water bath (80 x 60 x 21 cm) with water temperature maintained at 28.0 ± 0.1°C. The glass tank was separated into three compartments: a central compartment with a focal fish and two side compartments, with one side compartment containing a group of six conspecifics from an intermediate vulnerability phenotype, and the other side empty (Figure 2.3). To avoid spatial bias, the side compartment in which the group of conspecifics was placed was randomised. To avoid pheromonal or olfactory cues, the compartments were separated by fully sealed partitions that did not allow for transfer of water. A video camera (GoProHero 7) was mounted above the apparatus to record the behaviour of individuals during the trial.

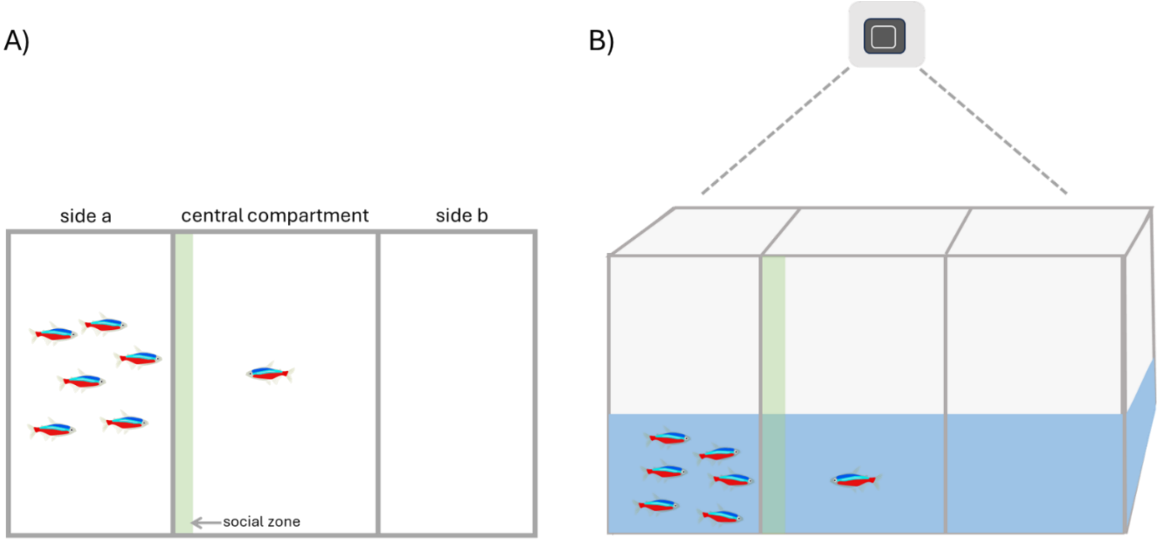

**Figure 2.3)** Schematic of individual sociability. A focal fish was placed into a central compartment. On either side of the central compartment there was a side compartment that contained either conspecifics or an empty zone. These were separated by a glass partition. A) view from above, B) three-dimensional view from the front.

At the start of each trial, conspecifics were randomly placed into side a or side b. The focal fish was placed into the central compartment inside the acclimation zone comprised of an opaque cylinder attached to a pulley system. After a 5-minute acclimation period, the cylinder was removed, and the fish was allowed to explore the area for 15 minutes.

### 2.3.4 Behavioural Traits: Video Analysis

All trials were recorded after the 5-minute acclimation period. Videos were analysed using Ethovision XT, version 15 (Noldus Information Technology, Inc). Sociability was quantified by totalling the number of seconds a focal individual spent in the social zone, which was an area defined within Ethovision next to the shoal of conspecifics (Figure 2.3A).

When the shelter was removed from arena, it was noted that some individuals would remain stationary, possibly as a stress-response. The time taken until an individual first moved from the shelter area was then recorded as latency to first move, which was used as a proxy for boldness. In some cases (n = 6) an individual would flee from the shelter and then freeze. In these cases, latency to first move was taken after the initial fleeing response.

Further measures of activity and exploration were also calculated using Ethovision. The time each focal individual spent moving was used as a proxy for activity. The total distance each focal fish covered within a trial was used as a proxy for exploration. Finally, the speed of focal fish whilst moving during the sociability assay was quantified by dividing the distance covered by the total time spent moving. All measured behavioural traits are summarised in Table 2.1.

**Table 2.1)** Descriptions of behavioural traits measured during video analysis.

| Behavioural trait | Description |
|---|---|
| **Sociability** | Total time spent in the social zone (s) |
| **Speed** | Distance travelled per unit of time (cm / s) |
| **Activity** | Total time spent moving (s) |
| **Exploration** | Distance moved (m) |
| **Boldness** | Latency to emerge from acclimation zone (s) |

### 2.3.5 Morphological and Physiological Traits

The swimming endurance of fish from the most and least vulnerable group was quantified by manually chasing fish in a circular tank (40 cm diameter, 10 cm water depth) by gently ushering fish to swim until exhaustion was reached, which was determined at the point where fish could no longer be motivated to swim (Killen et al., 2015). This method served as a proxy for fatigue by providing an insight into an individual's endurance. For each fish, wet mass (g), standard length (mm), and total length (mm) were also obtained. Individuals were not tagged in this experiment due to their small size, and to reduce the risk of tagging affecting subsequent observed behaviours. Wet mass was used to minimise air exposure and reduce stress and was measured to the nearest 0.01g. As the measurements were not done simultaneously, it was not possible to match an individual's size to its behavioural traits.

### 2.3.6 Statistical Analyses

#### 2.3.6.1 Vulnerability Assays

All analyses were conducted in R version 4.4.1 (R Core Team, 2022). To examine differences in the number of fish caught across trapping trials, a linear model was fitted with the percentage of individuals captured as the response variable, and fishing round (categorical) and temperature during the trial as explanatory variables. An additional model was fitted with entry latency as the response variable and fishing round as the explanatory variable. Model simplification was performed for both models using Akaike's Information Criteria (AIC) to identify the most parsimonious model.

#### 2.3.6.2 Behavioural Traits

The effect of behavioural traits; sociability, speed, activity, exploration, and boldness on capture vulnerability was assessed using generalised linear models (GLMs). Due to high collinearity between exploration and activity (Pairwise Pearson's r = 0.78), these variables were not included in the same model. Instead, two separate binomial GLMs were fitted with capture vulnerability as the response variable and sociability, boldness, speed, and either exploration or activity as explanatory variables. Assumptions of normality, linearity and homoscedasticity were verified by visual inspection of residual plots.

Predicted probabilities of capture were generated from the final GLMs using the ggpredict () function from the ggeffects package (Lüdecke, 2018), which estimates predicted values and confidence intervals for each behavioural predictor. Predictions were obtained for the significant variables; boldness, exploration, and activity individually.

To further understand the behavioural profiles of individuals used in the trials, and because the behavioural traits were correlated, I used a principal component analysis (PCA). PCA was performed on all five behavioural variables (sociability, boldness, speed, activity and exploration), which were centred and scaled. The prcomp () function in R was then used to apply singular value decomposition to the scaled data, which examines covariances among individuals. The PCA resulted in five principal component (PC) outputs. The proportion of variance captured by each principal component was examined to assess their overall contribution to the data (Figure 2.4). Based on the proportion of explained variation, the first two principal components (PC1 and PC2) were retained for further analysis. PC1 corresponded to a general activity and exploration axis and PC2 corresponded to a boldness and sociability axis. A binomial GLM was then fitted with capture vulnerability as the response variable and PC1 and PC2 as explanatory variables.

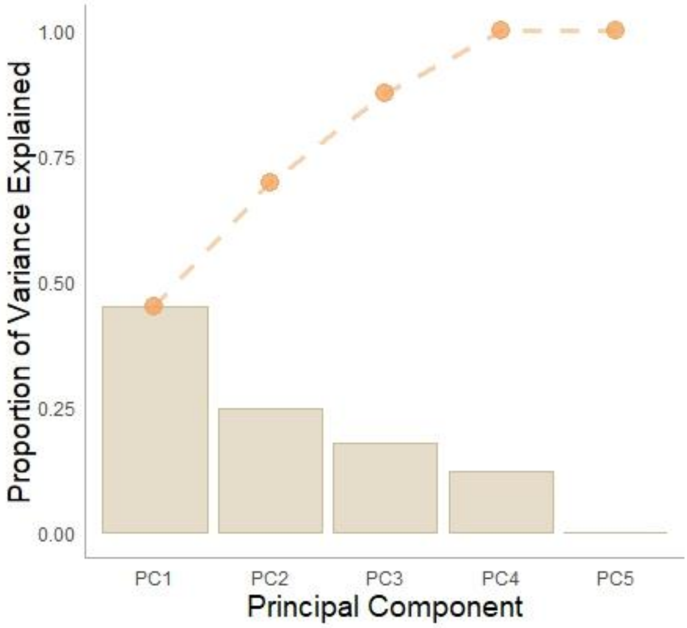

**Figure 2.4)** Scree plot showing the proportion of explained variation for the five principal components. The dashed line shows the cumulative proportion.

### 2.3.6.3 Morphological and Physiological Traits

To examine the effects of morphology and swimming performance on capture vulnerability, a GLM was fitted with a binomial distribution. Capture vulnerability (high or low) was used as the response variable with body mass and time until fatigue as explanatory variables. An interaction between mass and fatigue was also included in the model. Model simplification was then performed based on AIC values.

## 2.4 RESULTS

### 2.4.1 Vulnerability Assays

There were 33 fishing trials overall, with each trial composed of groups of fish starting from 40 in the first round and then ranging between 28-50 depending on the numbers of individuals left in each vulnerability category. At the end of the trials, there were 57 fish in the most vulnerable category (CCC) and 31 fish in the least vulnerable category (EEE). The remaining fish were an intermediate category that had been caught and escaped in separate rounds of fishing. Trial duration post-acclimation varied within and across treatments, ranging from 16 seconds to 570 seconds (mean ± SD: 168.9 ± 138.264s).

The percentage of fish that were captured by the trap varied across trials, with fewer individuals caught in round 2 (Figure 2.5; t -2.441, P = 0.021) and round 3 (Figure 2.5; t = -2.674, P = 0.012).

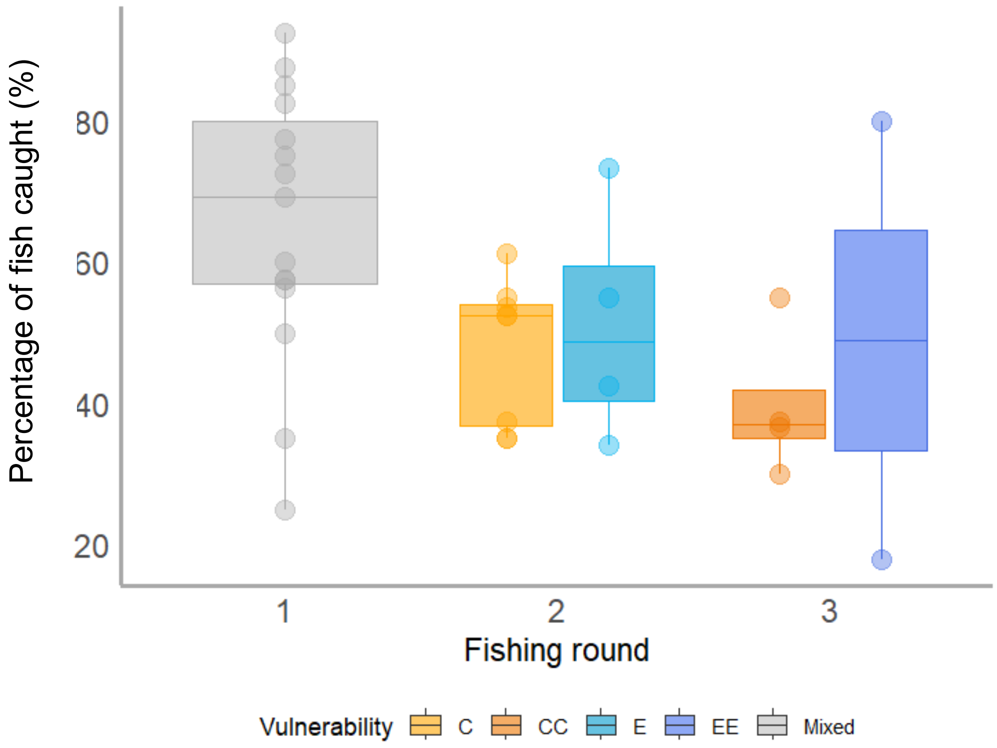

**Figure 2.5)** Percentage of fish captured in each round of fishing. One trial is made up of a group of 40 fish. Fishing round represents whether it was the first, second, or third time a group had been exposed to a trap. The colours represent the vulnerability category of the group. Grey represents fish from the first round, which had unknown vulnerabilities. Fish from the second round are comprised of individuals that had been either caught (C) or escaped (E) in the first round and fish from round 3 are comprised of individuals that had been caught (CC) or escaped (EE) in the second round. Each data point represents the percentage of fish captured in a fishing trial.

The time taken until the first fish entered the trap also varied across trials, however there was no significant difference in overall latency between fishing rounds (Figure 2.6, Supplementary Table 2.1).

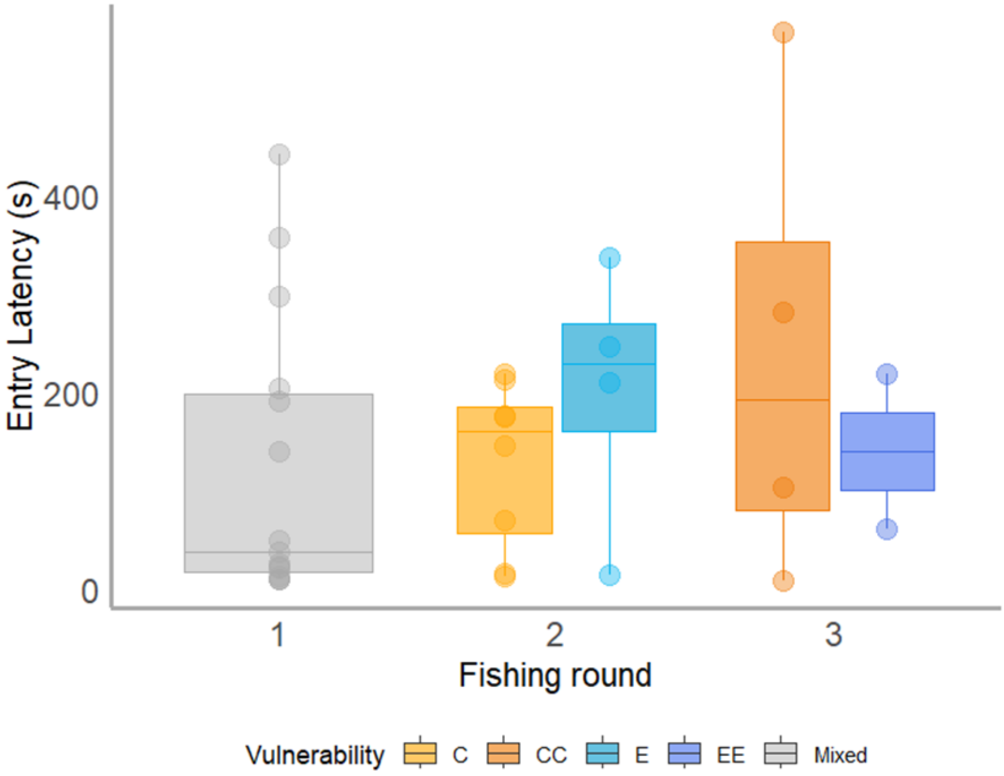

**Figure 2.6)** Time until first fish was captured during a trial in seconds. One trial is made up of a group of 40 fish. Fishing round represents whether it was the first, second, or third time a group had been exposed to a trap. The colours represent the vulnerability category of the group. Grey represents fish at the start of the first round, which had unknown vulnerabilities. Fish from the second round are comprised of individuals that had been either caught (C) or escaped (E) in the first round and fish from round 3 are comprised of individuals that had been caught (CC) or escaped (EE) in the second round. Each data point represents the latency of the first individual in a group to enter the trap within a trial.

### 2.4.2 Behavioural Traits

Sociability did not impact probability of capture as there was no significant difference in sociability between individuals with high and low vulnerability to capture (Supplementary Figure 2.1A; z = -0.423, P = 0.672). Similarly, speed was not related to capture vulnerability (Supplementary Figure 2.1C; z = 1.012 P = 0.312). In contrast, the predicted probability of capture was higher for individuals that were bolder and exhibited a shorter latency to emerge from the acclimation zone (Figure 2.7A; z = -2.812, P = 0.005). Additionally, individuals with a higher probability of capture were also more exploratory (Figure 2.6B; z = 2.429, P = 0.015) and more active (Figure 2.7C; z = 2.091, P= 0.036).

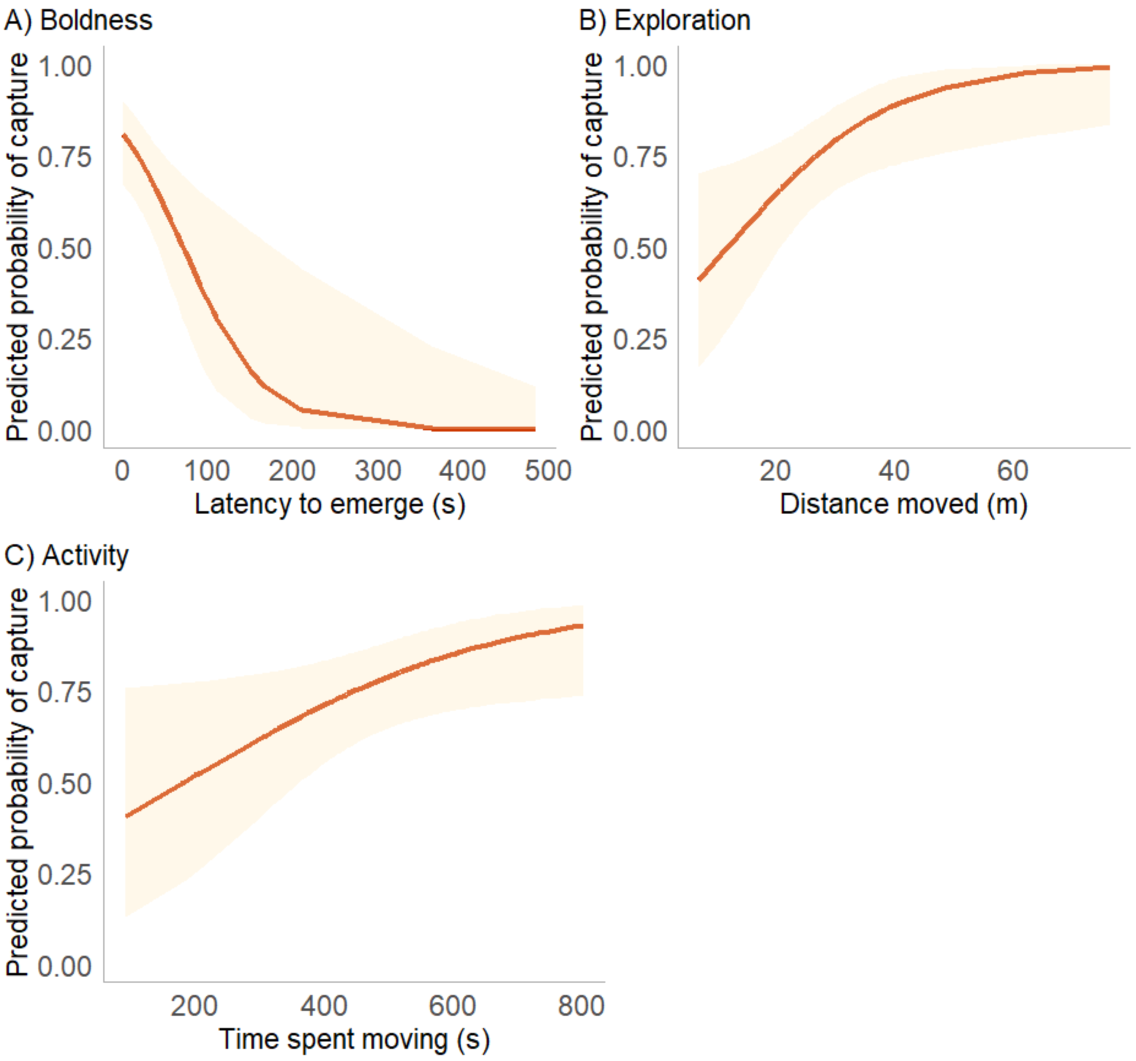

**Figure 2.7)** Predicted probability of capture as a function of behavioural traits: A) probability of capture as a function of boldness, measured by the latency to emerge from the acclimation zone; B) probability of capture as a function of exploration, measured by the total distance moved by an individual during a trial ; C) probability of capture as a function of activity, measured by the total time an individual spent moving during a trial. For all plots, the line represents the predicted relationship from the model, and the shaded region indicates the 95% confidence interval around the prediction.

The behavioural profiles of focal individuals were assessed using a PCA. The relationship between trait variables and principal components was visualised using a correlation heatmap (Figure 2.8A) and a biplot was generated to visualise the individual PCA scores and variable loadings (Figure 2.8B). The first principal component (PC1) represented a general activity axis, with positive loadings from speed, activity and exploration (Figure 2.8A). Boldness (latency) loaded negatively on PC1, with individuals scoring higher on PC1 having a shorter latency, and therefore a higher measure of boldness (Figure 2.8A-B). The second principal component (PC2) revealed an association between sociability and boldness (latency) (Figure 2.8B), where individuals that scored higher on PC2 were less social and had longer latencies to emerge (Figure 2.8A). Additionally, capture vulnerability was associated with PC1 scores, with more active individuals (high PC1) having a greater capture vulnerability (Figure 2.8C; z = 2.740, P = 0.006). In contrast, PC2 scores had no significant effect on capture vulnerability (Supplementary Table 2.3; z = 0.887, P = 0.375).

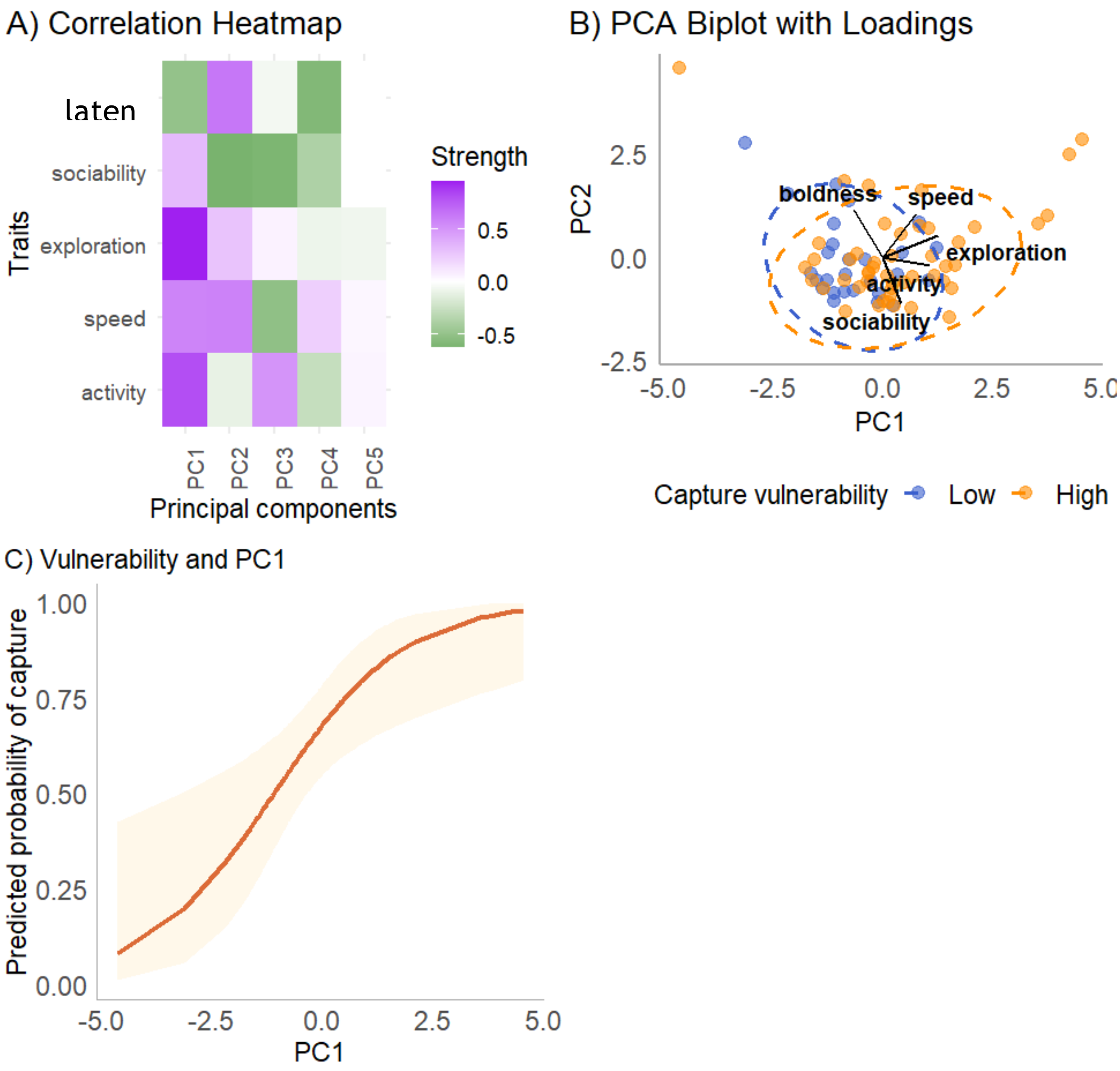

**Figure 2.8)** Principal component analysis (PCA) outputs: A) a correlation heatmap showing the strength and direction of relationships between variables and principal components. The strength and direction of the relationship is denoted by the colour, with purple corresponding to positive relationships and green corresponding to negative and greater opacity indicating greater strength; B) a biplot of PC1 and PC2 showing the PCA scores for different variables. Each point represents an individual, and lines represent the loadings of each behavioural trait to the PCA. The direction and length of each line indicates the strength and direction between the trait and the principal component. The points are grouped in clusters according to capture vulnerability; C) the impact of PC1 on capture vulnerability. The line represents the predicted relationship from the model, and the shaded region indicates the 95% confidence interval around the prediction.

### 2.4.3 Morphological and Physiological Traits

Smaller individuals had a greater vulnerability to capture (Figure 2.9A; z = -2.524, P = 0.012). Additionally, fish with shorter chase durations, and who fatigued faster, also had a higher vulnerability to capture (Figure 2.9B; z= -2.242, P = 0.025). Notably, there was no significant relationship between body mass and chase duration (Supplementary Table 2.4; z= -0.496, P = 0.620).

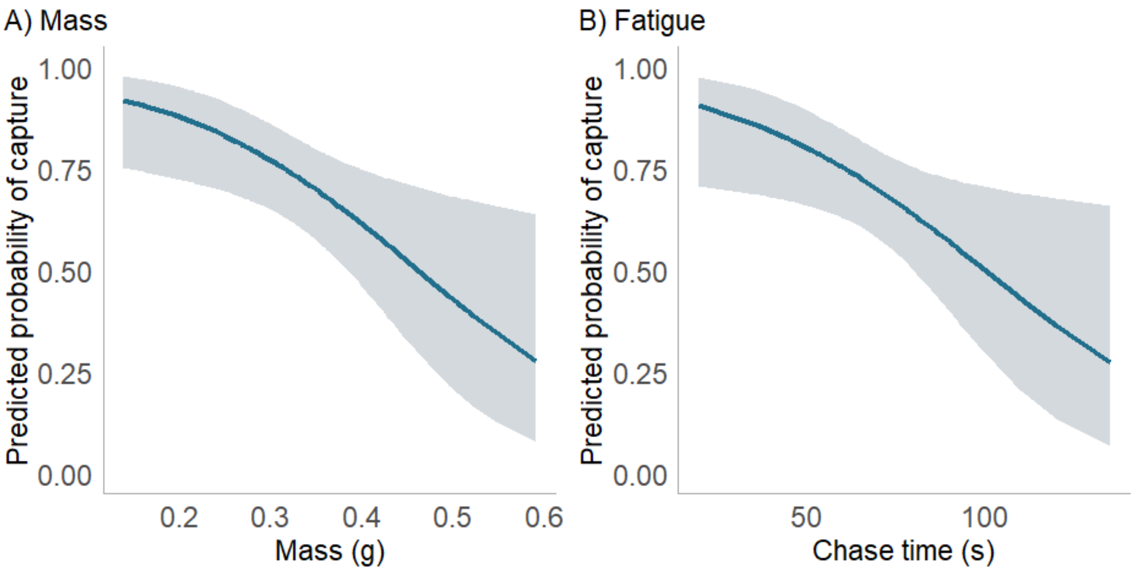

**Figure 2.9)** Predicted probability of capture as a function of morphological and behavioural traits: A) probability of capture as a function of body mass; B) probability of capture as a function of fatigue, measured by the duration of the chase before exhaustion was reached. For all plots, the line represents the predicted relationship from the model, and the shaded region indicates the 95% confidence interval around the prediction.

## 2.5 DISCUSSION

Understanding how individual phenotypes contribute to capture vulnerability is key to identifying which traits are most likely to be targeted by fisheries (Diaz Pauli and Sih, 2017; Killen and Koeck, 2023). While there has been a more recent shift towards understanding how behavioural and physiological traits relate to capture vulnerability in commercial and recreational fisheries, this had yet to be examined in a smaller-scale artisanal fishery. Here, I show that behavioural traits, namely boldness, exploration, and activity, and morphological and physiological traits such as size and endurance, predict vulnerability to capture in a popular ornamental species. For the first time, I show that there is therefore a potential for trait-based selection in the ornamental fishing industry.

Bolder individuals were more likely to be captured repeatedly, with latencies over 100s corresponding to a much lower probability of capture. Boldness is typically associated with a greater willingness to take risks and to explore novel stimuli, such as traps (Andersen et al., 2018; Biro and Dingemanse, 2008; Diaz Pauli et al., 2015; Diaz Pauli and Sih, 2017), which may explain the increased vulnerability in this study. Similarly, individuals that were more exploratory and more active also had a higher capture vulnerability. In commercial, recreational, and ornamental fisheries, the capture process can involve several behavioural stages: activity prior to trap discovery, approach, and trap entry (Thomsen et al., 2010). Across these stages, individuals that are bolder, more active, and more exploratory have an increased risk of capture (Andersen et al., 2018; Monk et al., 2021). As behavioural traits can have a heritable component (Dochtermann et al., 2015; Satterfield and Johnson, 2020), and consistently vary among individuals (Bell et al., 2009; Conrad et al., 2011), fishing pressure from artisanal traps could also cause long-term shifts in population-level behaviour. This aligns with the "timidity syndrome" proposed by Arlinghaus et al. (2017), which stipulates that over generations, populations become shyer, less active, and less exploratory overtime due to pressure from passive gears (Arlinghaus et al., 2017; Monk et al., 2021). In juvenile carp (*Cyprinus carpio*), boldness was the main trait under selection from hook-and line-angling (Klefoth et al., 2017). Similarly, angling selected against active individuals in rainbow trout (*Oncorhynchus mykiss*) (Koeck et al., 2019) and lure responsive individuals in largemouth bass (*Micropterus salmoides*) (Sutter et al., 2012). While the majority of studies have focussed on harvest selection in commercial and recreational fisheries, this study is the first to show that behavioural traits are related to capture vulnerability in a species targeted by the ornamental fishing trade.

Body mass also had an impact on capture vulnerability, where smaller individuals were more likely to be caught repeatedly. This may be linked to smaller fish being bolder (Brown and Braithwaite, 2004; Darby and McGhee, 2019; Ward et al., 2004). The relationship between size and boldness has previously been explained by the metabolic hypothesis that smaller fish have lower fat reserves and higher mass-specific metabolic rates and are therefore more compelled to forage in novel areas (Brown and Braithwaite, 2004). Negative correlations between body mass and boldness have been found in a range of animals, including poecilids (Brown and Braithwaite, 2004; Darby and McGhee, 2019), coho Salmon (Healey and Reinhardt, 1995), and hermit crabs (Briffa and Archer, 2023). Although I was unable to directly link individual behavioural traits to morphological and physiological traits in my study, the metabolic hypothesis remains a plausible explanation for the increased capture vulnerability of smaller fish. Size-selective fishing is an important driver of evolutionary change in commercial fisheries as it leads to reduced growth rates and other life history shifts (Heino et al., 2013; Uusi-Heikkilä et al., 2015). While commercial fisheries target larger fish, the opposite trend is typically true for ornamental fisheries, where smaller bodied individuals are often preferentially targeted or retained (OATA, 2020). Although the long-term impacts of size selective harvesting in the Amazon are currently not known, repeated capture of smaller, and often younger individuals could exert a strong selective pressure.

Fish that fatigued faster also had a higher vulnerability to capture, suggesting a reduced swimming performance. Generally, traits related to low swimming performance are typically associated with active gears such as trawls, as these pursue fish and are therefore more likely to target fish with reduced aerobic capacity and escape capabilities (Killen et al., 2015). In contrast, as passive gears capture individuals with increased movement and foraging behaviour, this is linked to a higher aerobic scope (Norin and Clark, 2016; Redpath et al., 2010). Fish with a higher aerobic scope are typically able to sustain more prolonged and active bursts of swimming (Hollins et al., 2018). However, in this study, fish that were more vulnerable could not sustain swimming activity, suggesting that these individuals may rely on short anaerobic bursts of activity, which may increase encounter rates with traps, but lead to faster exhaustion.

Notably, sociability had no impact on capture vulnerability in my study. This contrasts with previous findings, such as Thambithurai et al. (2018), which demonstrated that sociability underlies vulnerability to trapping, with fish in groups entering traps faster and spending longer inside. However, it does align with observations of sociability around traps in the Amazon, where spotted tetra (*Copella nattereri*), another popular ornamental species, showed limited evidence of sociability when entering traps (Pineda et al., 2025). Further work is therefore needed to determine if this is a consistent pattern that can be observed in more ornamental species.

When determining capture vulnerability, I found that although more individuals fell into the high vulnerability category rather than the low vulnerability category, overall, the highest number of individuals belonged to an intermediate category. The inter-individual variation in traits relevant to capture is a necessary requisite for selection to operate (Law, 2000). By focusing on individuals at the extreme ends of the vulnerability spectrum, I can identify which traits are more susceptible to fishing-induced selection. The repeated vulnerability assays also provided insight into how capture changed over successive fishing rounds. A greater number of fish were captured in the first round compared to the second and third. One possible explanation is that individuals in the first round of fishing were held in the same tanks prior to experiments and tested together. Their behaviours may therefore have been influenced by interactions with conspecifics with differing behavioural traits, which may have generated emergent effects on exploration and boldness (Jolles et al., 2020; Krause and Ruxton, 2010; Ward et al., 2004). Additionally, all individuals were naïve to the arena and the trap in the first round. In an unknown environment, some individuals may have perceived the trap as a shelter, a behaviour observed in other species when exposed to a novel structure (Burns and Rodd, 2008). Another possible explanation is that fish experienced learning or avoidance behaviour in response to the trap. This phenomenon has been observed in red sea bream (*Parus major*), where individuals avoided angling gear after only one or two catches (Takahashi and Masuda, 2021), as well as in common carp (*Cyprinus carpio* L.), where increased hook avoidance was found after repeated encounters (Klefoth et al., 2013). While ornamental fisheries do not operate recreational catch-and-release methods, intended bycatch can occur when fishers release non-target individuals. In such scenarios, it could therefore be possible for gear avoidance to occur, but this remains to be tested in ornamental fisheries in the wild.

Another important consideration is that only type of fishing gear was evaluated in this study. While it is clear that certain traits can predict capture vulnerability to a passive gear, the ornamental trade also uses an active gear (Chao, 2001; Prang, 2007). Future work is therefore needed comparing ornamental species caught by different gears to determine if the direction of trait-based selection is determined by gear type.

## 2.6 CONCLUSIONS

In summary, I used a simulated trapping scenario to show that individuals vary in capture vulnerability and that capture vulnerability is directly linked to behaviour, morphological, and physiological traits. Cardinal tetra that were bolder, more exploratory, and active, had a higher probability of repeated capture, as did fish that were smaller and fatigued faster. In contrast, I found no evidence of sociability nor speed influencing vulnerability to capture. However, I did observe a decline in the number of fish captured over successive fishing rounds, pointing to a potential for learning and gear avoidance in the cardinal tetra. This is phenomenon that has not yet been considered in the context of ornamental fisheries. To my knowledge, this is the first study to empirically show that individual phenotypes are linked to susceptibility to capture in the ornamental fishing trade. The findings of this chapter provide novel and valuable insight into how trait-based selection may operate in the ornamental trade and highlights the value of considering behavioural traits when assessing vulnerability. Finally, this study shows that even in a small-scale and non-consumptive fishery, non-random, trait-based selection could still occur.

# Chapter 3

# Differing selective effects on body size, swimming performance, and behaviour by passive and active fishing gears in an artisanal fishery

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## 3.1 ABSTRACT

There is increasing evidence that harvesting can selectively target and remove individuals with particular traits, driving phenotypic changes in wild populations. The type of fishing gear used can also play a critical role in determining which traits are targeted during harvest, influencing the direction of selection. While trait-based selection has been explored in commercial and recreational fisheries, the potential in smaller-scale artisanal fisheries, such as the ornamental fishing trade, remains virtually unexplored. Here, I investigated whether different artisanal gear types target specific behavioural and physiological traits in wild populations of cardinal tetra (*Paracheirodon axelrodi*), a popular ornamental species. Individuals were caught in the Amazon Basin using either a passive (trap) or active (net) artisanal gear type and transferred to the lab. The swimming performance of individuals was estimated using a constant acceleration test and behavioural phenotypes (risk-taking, exploration, activity, and group cohesion) were quantified using a suite of assays: open field, novel object, and maze tests. Trap-caught fish were significantly larger and had lower relative maximum swimming speeds than net-caught fish. Behavioural differences between gear types were revealed but varied depending on the assay used. Trap-caught individuals

exhibited greater risk-taking in the maze test, but there was no difference in risk-taking at the group level or in the open field and novel object tests. Net-caught fish were faster and spent more time together, but these patterns were also assay specific. Notably, even small variations in ambient temperature during trials significantly influenced behaviour, increasing activity and exploration, while reducing cohesion, suggesting sensitivity to climate change in fish. These findings are among the first to highlight the selective potential of artisanal gears across phenotypic traits, with repercussions for evolution and conservation. These findings also underscore the importance of considering assay design and environmental conditions when measuring behaviour.

## 3.2 INTRODUCTION

Human activities, such as harvesting, can have important repercussions for the survival, reproduction, and evolution of wild populations (Allendorf et al., 2008; Darimont et al., 2015; Hendry et al., 2017; Palkovacs et al., 2012). For example, harvesting often involves the selective removal of individuals with specific traits, from horn and antler size in large game animals (Coltman, 2008; Pigeon et al., 2016), to body size and growth in fishes (Enberg et al., 2009; Jørgensen et al., 2007). Indeed, harvest-associated selection is particularly well-documented in fisheries, where size-selective harvesting has resulted in smaller body size and earlier maturation across a variety of commercially exploited species (Enberg et al., 2012; Heino et al., 2015, 2013; Marty et al., 2015). While much of the research on fishing-induced selection has focussed on morphological and life-history traits (Ernande et al., 2004; Heino, 1998), there has been a recent shift towards understanding the impacts of fishing on the physiological and behavioural traits that render individuals more vulnerable to capture (Arlinghaus et al., 2017; Diaz Pauli et al., 2015; Diaz Pauli and Sih, 2017; Heino et al., 2015; Hollins et al., 2018a; Thambithurai et al., 2018).

Central to understanding how individual phenotype relates to capture vulnerability and subsequent fisheries-driven selection, is the type of gear used during capture (Biro and Dingemanse, 2008). Commercial and recreational fisheries employ a wide range of gear types, and they exist along a continuum of activity (Hollins et al., 2018a). Some gears, such as trawls and seines, are more active and directly pursue fish, and are therefore more likely to target traits related to reduced swimming performance and escape capability (Hollins et al., 2019; Killen et al., 2015). As active gears typically target large groups of schooling species, it is also possible that they may target traits related to sociability and group cohesion (Hollins et al., 2019; Thambithurai et al., 2018). In contrast, passive gears, such as traps and gillnets, rely on individuals voluntarily approaching and entering a gear, thus target traits related to foraging demand and willingness to take risks (Andersen et al., 2018; Arlinghaus et al., 2017; Claireaux et al., 2018). Despite growing interest in the selective effects of fishing gears, the majority of studies have examined active and passive gears in isolation. Very few studies directly compare the two gear types (but see Álvarez-Quintero *et al.,* 2021; Pauli *et al.,* 2015), limiting our ability to understand how gear selectivity can alter the phenotypic composition of exploited populations. Furthermore, existing studies have overwhelmingly focussed on either commercial or recreational fisheries, overlooking other sectors entirely, such as artisanal fisheries.

Artisanal fisheries are typically small scale, community-based operations that play a vital role in supporting food security and local economies across the globe (FAO, 2018, 2015; Júnior et al., 2016). While typically associated with subsistence fishing, artisanal fisheries also involve the capture of live fish for the ornamental trade, which harvests fish not for consumption, but for behavioural and aesthetic appeal in aquariums (Miller-Morgan, Tim, 2009). The ornamental fishing trade is a multi-billion-dollar global industry that is estimated to export over 1.3 billion fish annually, although the exact figure has been disputed (King, 2019). South America is one of the top exporters of freshwater fish, with many popular aquarium species being sourced directly from the wild due to difficulties with breeding fish in captivity (King, 2019). One of the most iconic and exported species in the ornamental trade is the cardinal tetra (*Paracheirodon axelrodi*), a small schooling fish endemic to the Amazon Basin (Evers et al., 2019; Tribuzy-Neto et al., 2021; Zehev et al., 2015). In the Amazon, particularly along the Rio Negro, fish are typically caught during the dry season, where larger tributaries dry into small streams known as *igarapés,* where water levels are low and fish are more concentrated. It is in these shallow streams that fishers use a variety of traditional artisanal gears, which also range from active to passive in their mode of capture. A typical example of an active gear is the *rapiché*, a large hand net fishers use to catch groups of fish immediately after visual detection (Chao et al., 2001; Prang, 2007). In contrast, the *cacurí* is a passive, baited cylindrical trap with a narrow entrance, typically deployed for longer periods (Prang, 2007). Both gears are designed to avoid damaging fish and are used to capture small characins such as cardinal tetra, though their use varies geographically, with *rapiché*s used in open streams of igarapes and *cacurís* used in shallow water with dense vegetation (Prang, 2007).

While the function of different artisanal gears has been documented, their potential for targeting specific phenotypes remains unknown. To date, no studies have quantified gear-associated trait differences in an artisanal fishery such as the ornamental fish trade, though it is possible that similar patterns to those observed in commercial and recreational fisheries may arise. For example, fish caught by *rapiché* may have reduced swimming performance, as individuals with reduced swimming performance or diminished escape responses are more susceptible to capture (Hollins et al., 2018a; Killen et al., 2015). Additionally, given that fish are typically captured after visual detection from fishers, it is possible that individuals that are more social, or more cohesive, may be more conspicuous and therefore more vulnerable to capture (Hollins et al., 2019). On the other hand, capture by *cacurí* may target riskier or more exploratory individuals as they are more likely to encounter and approach a novel structure (Álvarez-Quintero et al., 2021; Diaz Pauli et al., 2015). Similarly, fish with a higher foraging drive, or that are more active, may also have a higher likelihood of entering a passive gear. While these hypotheses are consistent with broader patterns of gear-associated selection, they have yet to be tested in an ornamental fishery.

To determine whether gear type influences the phenotypes of individuals in the ornamental fishing trade, I directly compared cardinal tetras caught with either an active or passive artisanal gear. Investigating phenotypic variation *in situ* can present complex challenges owing to environmental complexity and a lack of control. Thus, laboratory-based approaches offer the control necessary to untangle the contribution of individual traits to capture vulnerability, and to ascertain how different gears may exert selective pressures on physiological and behavioural phenotypes. In the lab, I assessed a suite of traits that have previously been linked to capture vulnerability. Specifically, I measured swimming performance using a constant acceleration test (CAT), an assay widely used to assess anaerobic capacity and endurance (Farrell, 2008). To determine behavioural phenotypes, I used a combination of behavioural assays to quantify common personality traits, namely risk-taking, exploration, group cohesion, and activity. As the type of assay used can elicit different behavioural responses (Colchen et al., 2017a; Way et al., 2015), and artisanal gears are typically used in habitats with differing structural complexity, I used a series of tests that increased in complexity, from an open field test, to a novel object test, to a maze test. To my knowledge, this is the first direct comparison of traits in fish caught by artisanal gears for the ornamental fishing industry. Specifically, I investigated: i) whether fish caught by active or passive gears differ in swimming performance and body size, and ii) whether they differ in behavioural traits, including risk-taking, exploration, activity, and group cohesion. Based on prior findings from commercial and recreational fisheries, I hypothesised that fish caught by nets would have a reduced swimming performance, but would be more cohesive, while fish caught by traps would exhibit higher levels of risk-taking and be more exploratory. Understanding whether artisanal gears target different phenotypes is an important step toward assessing the potential for fishing-induced selection in ornamental fisheries, which has implications not only for the sustainability of trade, but for the livelihoods of the individuals that rely on wild-sourced aquarium species.

## 3.3 METHODS

### 3.3.1 Fish Collection and Husbandry

Cardinal tetras (*Paracheirodon axelrodi*) were collected from tributaries of the Rio Negro in Barcelos, Brazil (Paraná do Saia; 0°56'56.4"S 62°41'49.5"W). The municipality of Barcelos is often described as the hub of ornamental fishing in the Brazilian Amazon, due to the historic legacy of wild capture, as well as the cultural and economic importance to local communities (Evers et al., 2019; Ferreira and Yamamoto, 2017; Ladislau et al., 2020; Zehev et al., 2015). Sampling was done over three days in September 2022, each morning, using either a traditional trap, *cacurí*, baited with fish, or a modified net, *rapiché,* commonly used by ornamental fishers. The trap consisted of a fine mesh shaped into a cylinder with a narrow opening (Figure 3.1A) and the net consisted of a fine mesh shaped into a large, modified hand net (Figure 3.1B). Around 250 individuals were caught using the trap and 450 using the net. Environmental variables: air temperature, water temperature, pH, and dissolved oxygen, were measured at each sampling site (see Supplementary Table 3.1). After fishing, only cardinal tetras were retained, and all other non-target species were released. At the end of each day, cardinal tetras were then transported by boat back to Barcelos and held in separate storage tanks according to capture method. Transport time from the field site to the holding area was ~ 1 hour. The permit for the collection of the biological material to carry out the research was authorized by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA/SISBIO), number 29837-13.

**Figure 3.1)** Artisanal gears used to capture ornamental species, such as cardinal tetra: A) *cacurí* - a cylindrical trap made of fine mesh (45 x 28 cm) with a narrow funnel-shaped opening (5 cm wide); B) *rapiché*- a modified hand net (97 x 45 cm). Photos by S. S. Killen.

Once all fish had been collected, they were transported by boat to aquarium facilities at the National Institute for Amazonian Research (INPA) in Manaus. Transport time between Barcelos and Manaus was ~15 hours, with fish monitored throughout the transport period. At INPA, fish were housed in 250 L circular tanks maintained at 26 ± 1.5°C, with a natural photoperiod (±12:12 h light-dark), and were fed commercial feed *ad libitum*. Following a one-week acclimation period, experiments were conducted to investigate whether capture method influenced physiological and behavioural traits. Four experiments were conducted: a constant acceleration test, a maze test, an open field, and a novel object test. To minimise order effects caused by fatigue, individuals used in the constant acceleration test were not reused in the behavioural assays. Some individuals were reused across the behavioural tests, but never within the same type of behavioural assay, ensuring each fish was naïve to the specific experimental setup. When fish were reused for behavioural tests they were given at least three days between trials. For all trials, water temperature was measured at the start of each trial and water was changed between trials to minimise pheromonal cues (Fontana et al., 2021). All experimental procedures were approved by the Animal Use Ethics Committee of the Brazilian National Institute for Research of the Amazon (CEUA-INPA), number 01280.000209/2018-74.

### 3.3.2 Constant Acceleration Tests

A total of 20 (n = 10 groups per capture method) constant acceleration tests (Farrell, 2008) were conducted using a 5 L Brett-style swim tunnel (Loligo Systems, Denmark; swimming chamber 28 x 7 cm; Figure 3.2). Each trial tested a group of six unmarked fish. Individuals were netted from holding tanks and transferred to the swim tunnel, where they were given a 5-minute acclimation period at a low baseline water velocity (10 cm $s^{-1}$). After acclimation, water velocity was increased in a stepwise manner, with increments of 1 cm $s^{-1}$ every 30 seconds. The protocol continued until all individuals in the group reached exhaustion, defined by an individual resting against the back grid of the working section of the swim tunnel. For each fish, the time taken until exhaustion was recorded, as well as their maximum swimming speed (cm/s). At the end of a trial, all fish were measured for standard length (SL) and total length (TL). As fish were untagged and could not be individually removed from the swim tunnel during the trial, it was not possible to match an individual's maximum swimming speed to its length. Therefore, all individuals were size matched before the trial started and SL and TL were averaged for each group. For all trials, max swimming speed was divided by the average standard length of the group to provide a measure for body lengths per second (BL/S). Although both TL and SL are useful measures of length in fish, SL was ultimately chosen as a baseline to account for differences caused by caudal fin shape or length, a feature which can be especially variable in ornamental species.

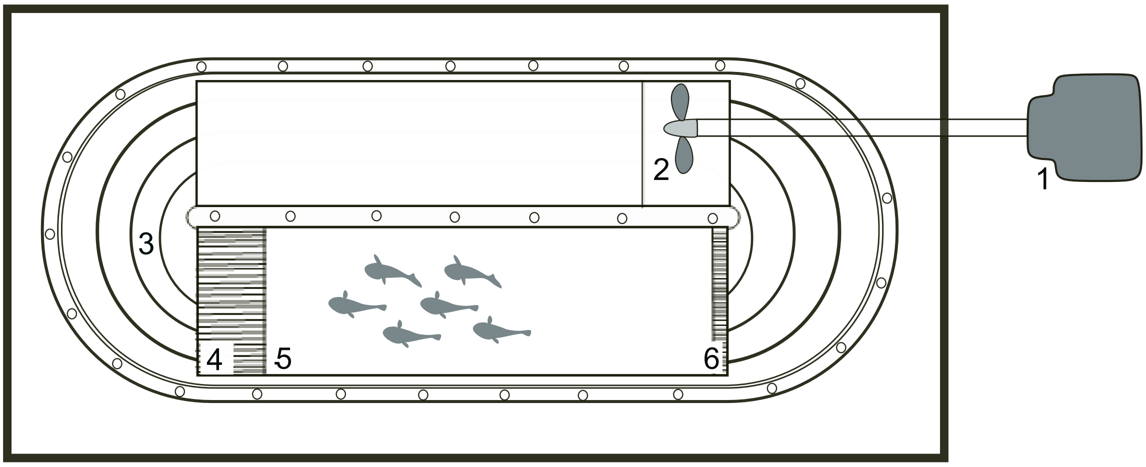

**Figure 3.2)** Schematic of Brett-type swim tunnel used to determine maximum swimming speed of fish caught by different gear types. View from above: 1) motor; 2) propellor; 3) flow straightening vanes; 4) honeycomb grid for laminar flow; 5) enclosed swimming chamber; and 6) back grid. Adapted from Mittún et al., (2025).

### 3.3.3 Maze Tests

Two identical mazes were built for the behavioural measures. Each maze was enclosed in a white, opaque rectangular arena (60 x 42 cm) with alternating walls positioned along the length of the arena to create five maze levels (Figure 3.3). The walls were 10 cm high, and water depth was maintained at 6 cm during trials. Each maze began with a starting chamber, which served as an acclimation zone. Fish were tested in groups of six, a commonly used number in behavioural studies (Anderson et al., 2020; Hockley et al., 2014; Latchem et al., 2025; Lonhus et al., 2023), given that it is a large enough number that social dynamics can be observed in a group, while being manageable for video analysis and reliable tracking of individuals. Groups were introduced into the starting chamber and given a 5-minute acclimation period. After acclimation, the door was removed from the starting chamber by hand, and fish were allowed to explore the maze freely for 15 minutes. All trials were recorded with a video camera (GoPro Hero 4) mounted above the arena. Between trials, water in the maze was emptied and replaced to eliminate chemical or social cues that could influence the behaviour of fish in subsequent groups. A total of 36 maze trials were conducted overall (n = 18 trials per capture method).

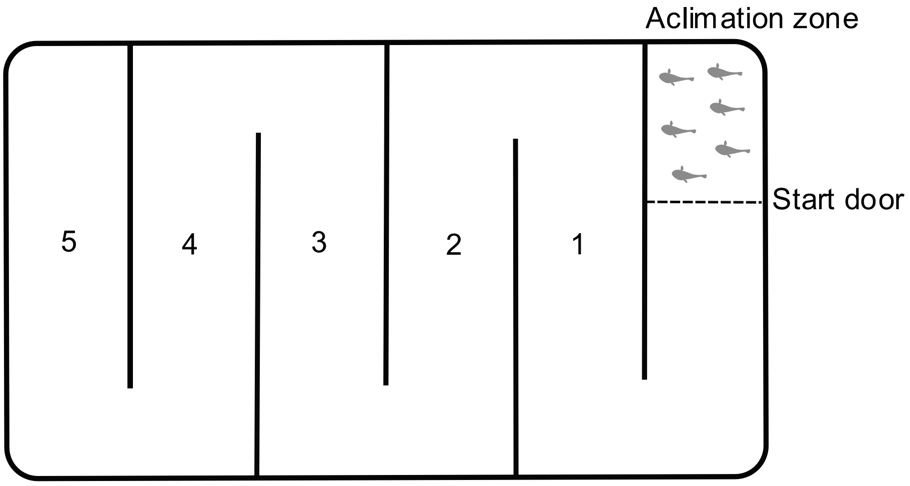

**Figure 3.3)** Schematic of maze used to measure behavioural traits of cardinal tetra caught by different gear types. The acclimation zone is labelled at the start of the maze. The removable starting door is labelled and denoted by a dashed line and the different levels of the maze are labelled.

Video analysis was then conducted using Solomon Coder (version 19.08.02) to quantify four behavioural traits: risk-taking, exploration, and cohesion. Data were extracted at the group level and for individual fish within groups (Table 3.1).

**Table 3.1)** Descriptions of behavioural traits measured in the maze test.

| **Behaviour** | **Description** |
|---|---|
| Risk-taking | Time taken (in seconds) for a fish to emerge from the acclimation zone. Measured for the first fish within a group to merge as well as the average emergence time of the whole group during a trial. |
| Exploration | Time taken (in seconds) for each individual and the entire group to complete the maze. If a fish or group did not complete the maze, a maximum time of 21 minutes was assigned. The time taken for fish to emerge from the starting chamber was subtracted from the time taken to complete the maze. |
| Cohesion | Percentage of time fish spent swimming as a group as opposed to fragmented. A group was considered fragmented if they were more than five body lengths apart, or in separate maze levels, for over five seconds. |

### 3.3.4 Open Field and Novel Object Tests

Open field and novel object tests were conducted in a rectangular arena (60 x 40 cm) filled with water to a depth of 6 cm. Water temperature was maintained at 26 ± 1.5 °C across all trials. At the start of each open field trial, a group of six fish was introduced into an opaque cylindrical acclimation zone located in the centre of the arena. Following a 5-minute acclimation period, the tube was gently removed, and fish were allowed to explore the arena freely for 5 minutes.

Immediately after the open field phase, a small submergible toy (7 x 5 cm) was introduced into the arena for the novel object test. The novel object was placed in a fixed location across trials to ensure consistency. Fish were then allowed to explore the arena freely for an additional 10 minutes. After each trial, the water was fully replaced to eliminate chemical social cues, and all individuals were measured for standard length (SL) and total length (TL). A total of 36 open field and 36 novel object trials were conducted (n = 18 trials per capture method for both the open field and novel object test), and all trials were recorded using a video camera (GoPro Hero 4) mounted above the arena.

Videos were analysed using Ethovision XT 15 (Noldus Information Technology, Wageningen, The Netherlands). For open field trials, analysis began 30 seconds after the start of the trial, to account for any disturbance caused by removing the acclimation zone. Data were extracted for each individual for 4 minutes. For the novel object test, video analysis began 30 seconds after the novel object was placed into the arena to account for any disturbance caused by placing the novel object. The novel object videos were analysed for a total of 6 minutes.

Individual-level movement data were extracted for each fish within the group to quantify behavioural metrics listed in Table 3.2. Due to repeated issues with reliably tracking certain individuals, 5 open field trials included data for only 4-5 fish, and 4 novel object trials included data for 5 individuals instead of 6.

**Table 3.2)** Summary of behavioural metrics extracted from video analysis.

| **Behaviour** | **Description** |
|---|---|
| Risk-taking $_{\text{Arena}}$ | Mean distance (cm) from a fish to the centre of the arena. |
| Risk-taking $_{\text{Novel Object}}$ | Mean distance (cm) from a fish to the novel object. |
| Exploration | Total distance (cm) moved by an individual. |
| Activity | Average moving speed (cm $s^{-1}$), calculated as total distance moved divided by time spent moving. |

| | |
|---|---|
| Cohesion | AND: Average neighbour distance (cm), defined as the mean distance between an individual and all other group members. |

### 3.3.5 Statistical Analyses

All statistical analyses were carried out in R (version 4.4.1).

#### 3.3.5.1 Constant Acceleration Tests

To examine differences in body size between cardinal tetra caught with different gear types, independent two-sample t-tests were carried out for both standard length and total length. To assess swimming performance, a series of linear models were used. The first model used maximum swimming speed in body length per second (BL/S) as the response variable, with mode of capture and temperature as explanatory variables with an interaction between them along with standard length. As fish were unmarked, it was not possible to link an individual's body length to its swimming performance. Instead, the mean standard length of the group was used, as fish within groups were size matched. A further model used time until exhaustion as the response variable, with the same explanatory variables. For both models, model simplification was performed in a stepwise manner by sequentially removing variables based on Akaike Information Criterion (AIC) values.

#### 3.3.5.2 Maze Tests

Behavioural data extracted from the maze tests were analysed using a series of linear models. Risk-taking was quantified as the latency in seconds for fish to emerge from the acclimation zone. Two models were run: one using the latency of the first individual within a group to emerge, and another using the average latency of all individuals to emerge. For both models, latency was used as the response variable, with mode of capture, test temperature, average group body size, and an interaction between mode of capture and test temperature included as explanatory variables. Exploration was quantified as the time taken in seconds to complete the maze. Two models were fitted, one with the time taken for the first individual to complete the maze as a response variable, and another with the average time for all individuals to complete the maze as the response variable. For both models, mode of capture, test temperature, average body size, risk-taking, and group cohesion were included as explanatory variables. An interaction between mode of capture and cohesion was also included. Cohesion was measured as the percentage of time individuals spent in close proximity to conspecifics as the response variable. Mode of capture, temperature, average body size, and risk-taking were used as explanatory variables. For all models, model simplification was performed in a stepwise manner by comparing AIC values. To test whether body size differed between capture methods, a Welch two-sample t-test was used.

#### 3.3.5.3 Open Field and Novel Object Tests

Behavioural metrics collected from the open field and novel object tests were analysed with linear mixed-effects models using the lme4 package (Bates et al., 2015). Activity, average neighbour distance, and risk-taking were used as response variables. Fixed effects included temperature, mode of capture (net or trap), and experiment type (open field or novel object). An interaction between treatment and experiment type was also included to test whether fish caught by different gear types exhibit different behavioural responses depending on experimental context. As the same groups were used across both tests, group was included as a random effect. Individuals were unmarked and Ethovision did not maintain consistent individual identities across experiment types; therefore, individual was not included as a random effect. Data from the open field and novel object tests were combined for these analyses, as the response variables were averaged, and therefore unlikely to be influenced by differences in trial duration between the experiment types. Combining datasets enabled direct comparison of behaviour between the open field and novel object tests. For behavioural metrics where trial length could influence the outcome of behaviour, such as total distance covered, data were subset by experiment type and analysed separately. Data were also subset for risk-taking $_{NO}$, as this behavioural measure was only applicable to the novel object test. In these two cases, linear mixed-effects models were fitted with total distance covered and distance to the novel object as response variables. Temperature and mode of capture were again included as the explanatory variables and group was used a random effect. Model selection was performed in a stepwise manner, using likelihood ratio tests to identify the most parsimonious models for each response variable.

## 3.4 RESULTS

### 3.4.1 Constant Acceleration Tests

Individuals caught by different gear types had significant differences in body size (Figure 3.4). Fish caught by traps were significantly larger in both standard length (Figure 4A; independent t-test: t = -5.55, df = 116.64, $p < 0.001$) and total length (Figure 3.4B; independent t-test: t = -2.95, df = 114.68, p = 0.004) compared to individuals caught by nets.

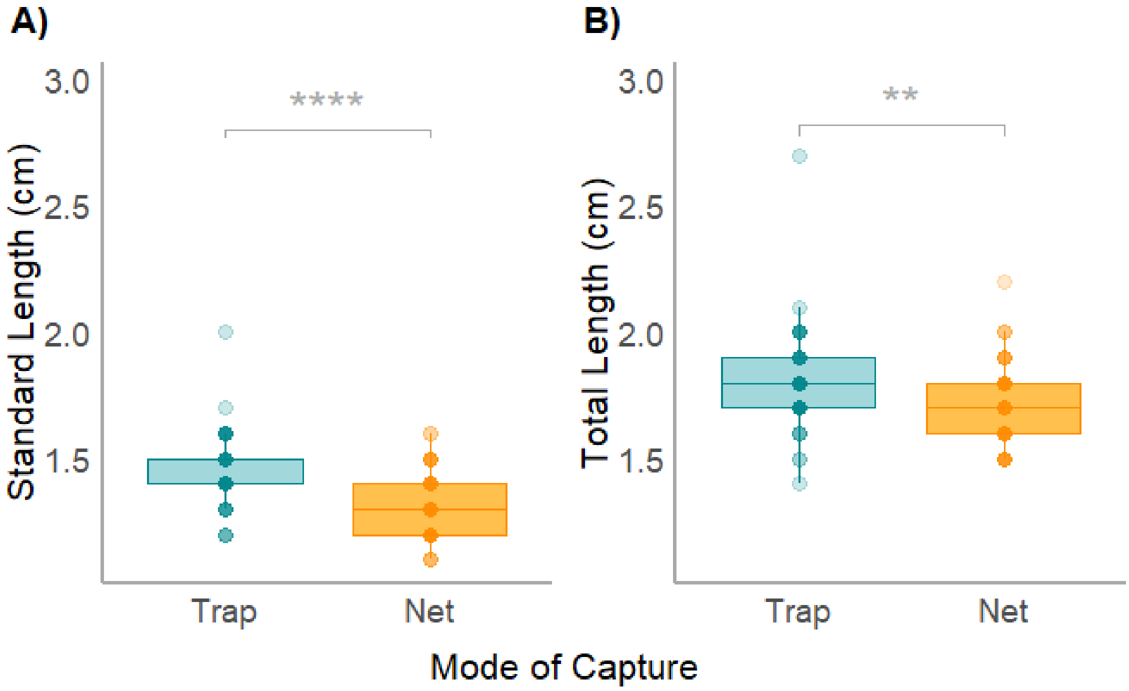

**Figure 3.4)** Body length of individuals caught by traps and nets. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****). A) Standard length of fish caught by traps (blue) or nets (orange). Each data point represents an individual. B) Total length of fish caught by traps or nets. Each data points represents an individual.

Swimming performance was determined by measuring the time until exhaustion and maximum swimming speed of individuals, corrected for body size. Individuals captured using traps had a lower maximum swimming speed than those caught by nets (Figure 3.5A; Estimate = -1.25 ± 0.47 SE, t = -2.68, p = 0.008). There was no evidence that temperature during the trial (Supplementary Table 3.2; Estimate = 1.03 ± 0.62 SE, t = 1.66, p = 0.099) nor mean standard length (Supplementary Table 3.2; Estimate = 0.89 ± 3.46 SE, t = 0.26, p = 0.798) influenced the swimming speed of individuals. Additionally, there was weak evidence that time until exhaustion differed between individuals caught by different gears (Figure 3.5B; Estimate = 96.39 ± 51.93 SE, t = 1.86, p = 0.066). However, time until exhaustion was influenced by body length, with time until exhaustion increasing with mean standard length (Figure 3.5B; Pearson's r = 0.28, t = 3.13, p = 0.002, 95% CI [0.10, 0.44]).

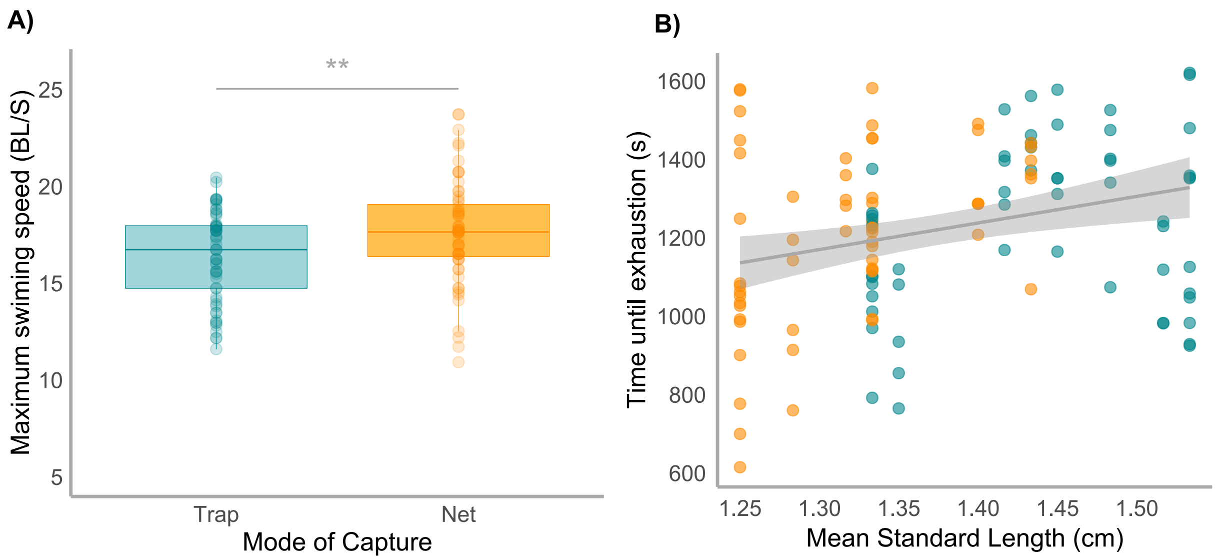

**Figure 3.5)** Swimming performance of fish caught by traps and nets. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****). A) Maximum swimming speed in body lengths per second of fish caught by traps (blue) or nets (orange). Each data point represents an individual. B) Scatter plot showing the relationship between time until exhaustion and mean standard length for fish caught by traps (blue) and nets (orange). The solid line indicates the linear regression fit, with the shaded region indicating the 95% confidence intervals.

### 3.4.2 Maze Tests

Risk-taking of groups and individuals within a group was quantified by measuring the time taken in seconds (latency) for fish to emerge from the acclimation zone. For the first individual to emerge, fish caught by traps emerged around 24 seconds faster compared to those caught by nets (Figure 3.6A, Estimate = -23.61 ± 9.65 SE, t = -2.45, p = 0.020). However, at the group level, there was no difference in latency between fish caught with different gear types (Figure 3.6B, Estimate = -1035.58 ± 659.57 SE, t = -1.57, p = 0.127). There was also no evidence that body length influenced risk-taking at the individual

(Estimate = -5.40 ± 31.72 SE, t = -0.17, p = 0.866) or group level (Estimate = 26.39 ± 36.53 SE, t = 0.72, p = 0.475).

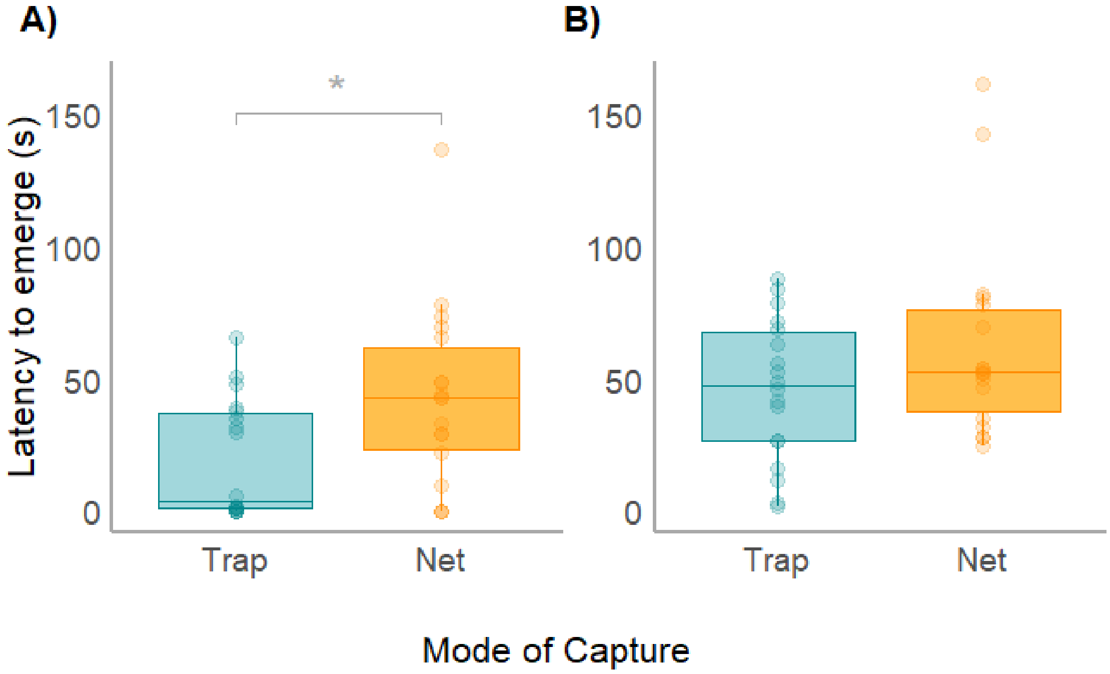

**Figure 3.6)** Risk-taking, measured as latency to emerge from acclimation zone, for fish caught by traps and nets. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****). A) Latency of the first individual within a group to emerge from the acclimation zone. Each data point represents an individual. Shorter latency times indicate higher levels of risk-taking. B) Latency of the whole group to emerge from the acclimation zone. Each data points represents the mean latency of a group during a trial, with shorter latencies indicating higher levels of risk-taking.

The time taken to complete the maze was also recorded for the first individual within each group and for the group as a whole. There was no evidence that time taken for the first individual to complete the maze was influenced by any of the model predictors (all $p > 0.3$; Supplementary Table 3.3). In contrast, mean completion times of groups differed between gear types, and was also influenced by group cohesion. On average, fish caught by nets completed the maze faster than those caught by traps (Figure 3.7A; Estimate = 660.39 ± 295.55, t = 2.23, p = 0.033). Additionally, there was a significant interaction between capture method and group cohesion (Estimate = -13.92 ± 4.96 SE, t = -2.81, p = 0.008), revealing that the relationship between maze completion and group cohesion was dependent on the gear type used (Figure 3.7B). Specifically, net-caught fish completed the maze faster when they were more cohesive, whereas trap-caught fish completed the maze faster when they were less cohesive.

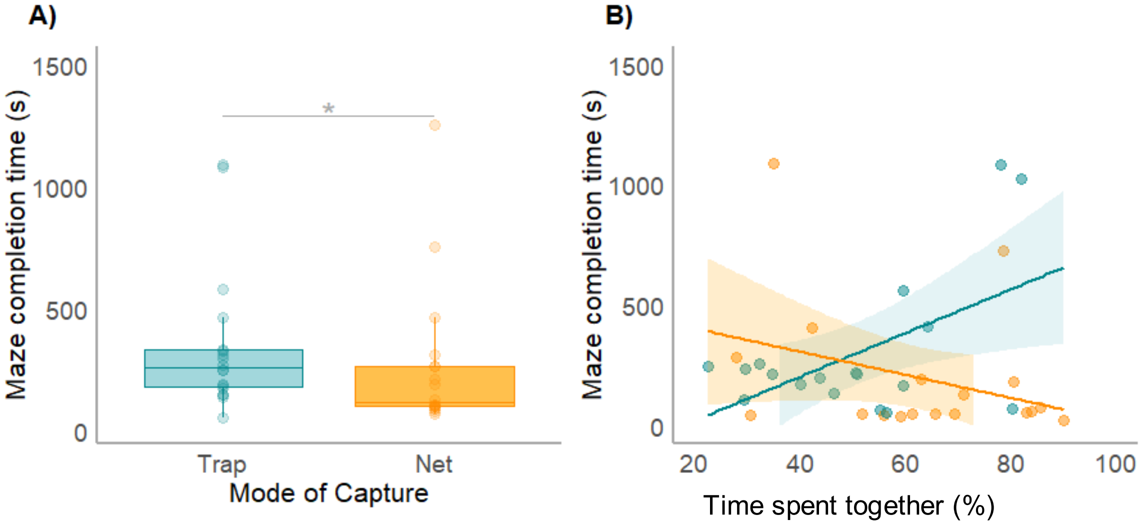

**Figure 3.7)** Maze completion times of fish caught by different gear types, and the relationship between maze completion time and cohesion. A) Time taken for fish caught by traps (blue) and nets (orange) to complete the maze. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: p < 0.05 (*), p < 0.01 (**), p < 0.001 (***), p < 0.0001 (****). Each data point represents the average maze completion time of a group within a trial. B) The relationship between maze completion time and the percentage of time spent as a group within a trial for fish caught by nets and traps. Trend lines represent the predicted values from the linear model, and the shaded regions represent the 95% confidence interval.

Group cohesion differed between fish caught by different gear types, with net-caught individuals spending more time together during trials compared to those caught by traps (Figure 3.8A; Estimate = 13.59 ± 6.01 SE, t = 2.26, p = 0.031). There is also evidence that temperature during trials had a significant impact on group cohesion, with groups becoming less cohesive as temperatures increased (Figure 3.8B; Estimate = -14.39 ± 6.72, t = -2.14, p = 0.040). However, there was no evidence that the relationship between temperature and group cohesion differed according to capture method (Estimate = 21.78 ± 16.11, t = 1.35, p = 0.187).

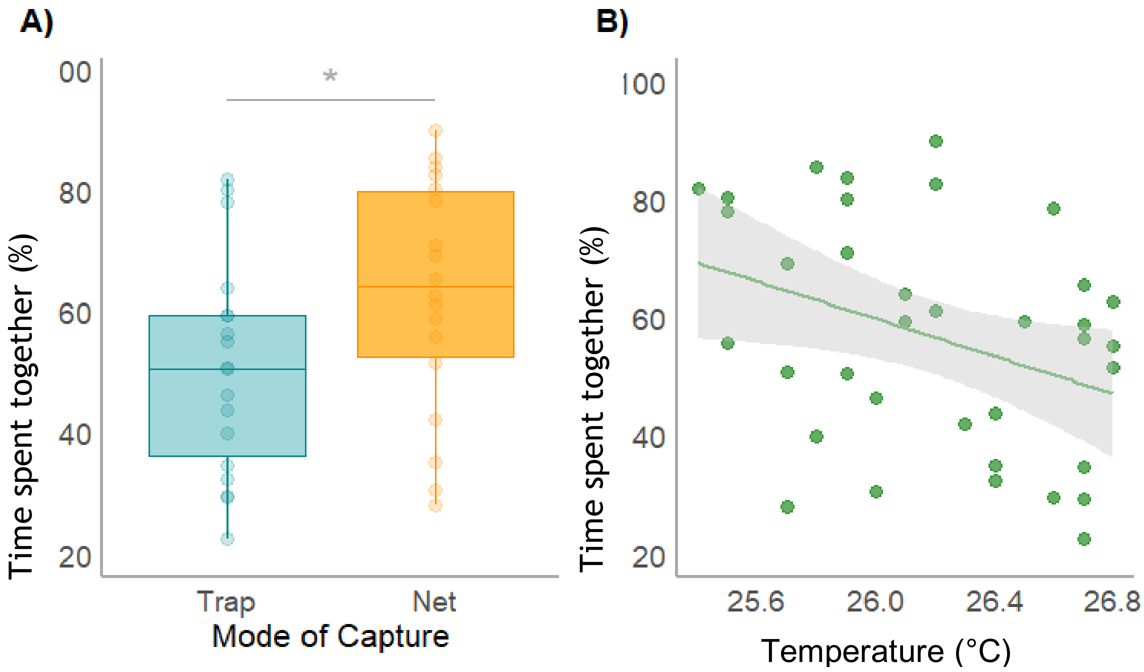

**Figure 3.8)** Group cohesion of fish caught by different gear types and the relationship between temperature and group cohesion. A) Percentage of time groups caught by traps (blue) and nets (orange) spent together in a trial, as opposed to fragmented. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****). Each data point represents the percentage of time for one group. B) The relationship between group cohesion and temperature (°C) during the trial. Trend lines represent the predicted values from the linear model, and the shaded regions represent the 95% confidence interval. Each data point represents a group.

### 3.4.3 Open Field and Novel Object Tests

Fish caught by different gears exhibited differences in group cohesion. Fish caught using nets maintained shorter average distances to their conspecifics, compared to those captured using traps, indicating higher group cohesion in the open field and novel object test (Figure 3.9; Estimate = –1.27 ± 0.59 SE, $t = –2.15$, $df = 69.79$, $p = 0.035$). However, there was no evidence that cohesion differed between the open field and novel object tests (Supplementary Table 3.4; Estimate = 0.43 ± 0.82 SE, $df = 66.83$, $t = 0.53$, $p = 0.601$) and no evidence of an interaction between mode of capture and experiment type (Estimate = 0.54 ± 1.19, $df = 66.84$, $t = 0.45$, $p = 0.653$), indicating that the observed effect was consistent across both experiment types.

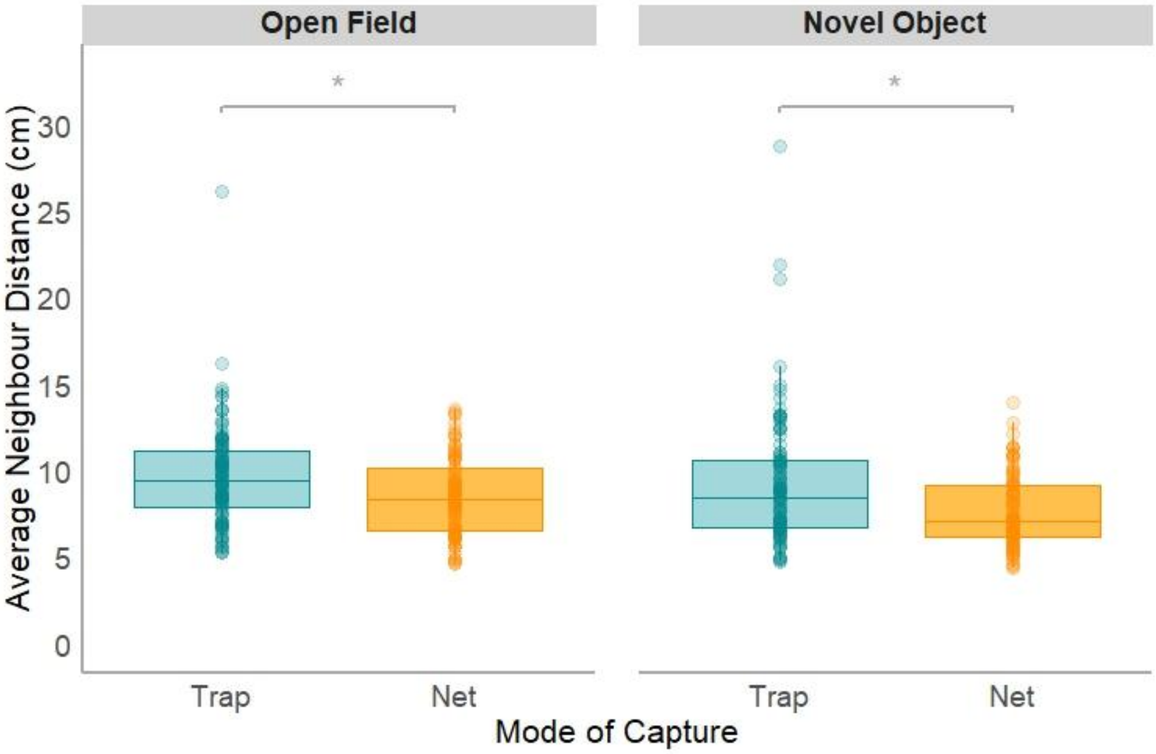

**Figure 3.9)** Group cohesion, measured as average neighbour distance (AND), between fish caught by different gear types during open field and novel object tests. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****). Each data point represents the average neighbour distance of an individual and points outside of the range of the whiskers are shown as outliers.

Fish caught by different gears also exhibited differences in activity, quantified as average moving speed. Fish caught using nets were faster than those caught using traps (Estimate = 0.86 ± 0.39 SE, df = 67.94, t = 2.23, p = 0.029). Temperature during the trial also influenced speed, with individuals moving faster at higher temperatures (Figure 3.10; Estimate = 1.14 ± 0.44 SE, df = 67.91, t = 2.62, p = 0.011). Experiment type also influenced speed, with individuals moving more slowly in the novel object test compared to the open field test (Figure 3.10; Estimate = 0.77 ± 0.38, df = 67.94, t = 2.01, p = 0.049).

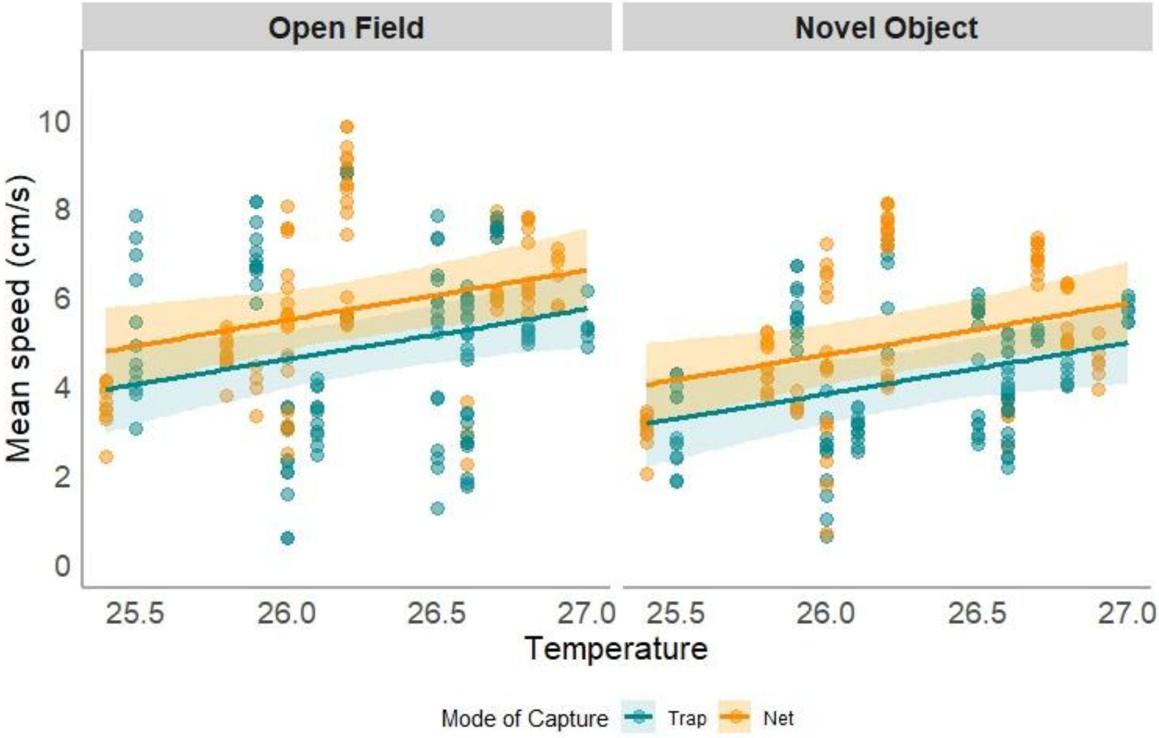

**Figure 3.10)** The relationship between temperature (°C) and mean speed of individuals caught by traps (in blue) and nets (in orange) in open field and novel object tests. Each data point represents the average speed of an individual fish during a trial. Trend lines represent the predicted values from the linear-mixed effects model, and the shaded regions represent the 95% confidence interval. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****).

In the open field test, there was no evidence that exploration (measured as total distance travelled) differed between gear types (Figure 3.11A; Estimate = 206.15 ± 156.7 SE, df = 32.97, t = 1.32, p = 0.198). There was also no evidence that temperature influenced exploration (Estimate = 271.07 ± 177.32 SE, df = 32.96, t = 1.53, p = 0.136). In contrast, during the novel object test (Figure 3.11B), while there was weak evidence that exploration differed between fish caught by different gears (Estimate = 362.83 ± 192.77, df = 32.99, t = 1.88, p = 0.069), there was a relationship between exploration and temperature, with individuals covering a greater distance at warmer temperatures (Figure 3.11B; Estimate = 519.65 ± 218.07 SE, df = 32.98, t = 2.38, p = 0.023).

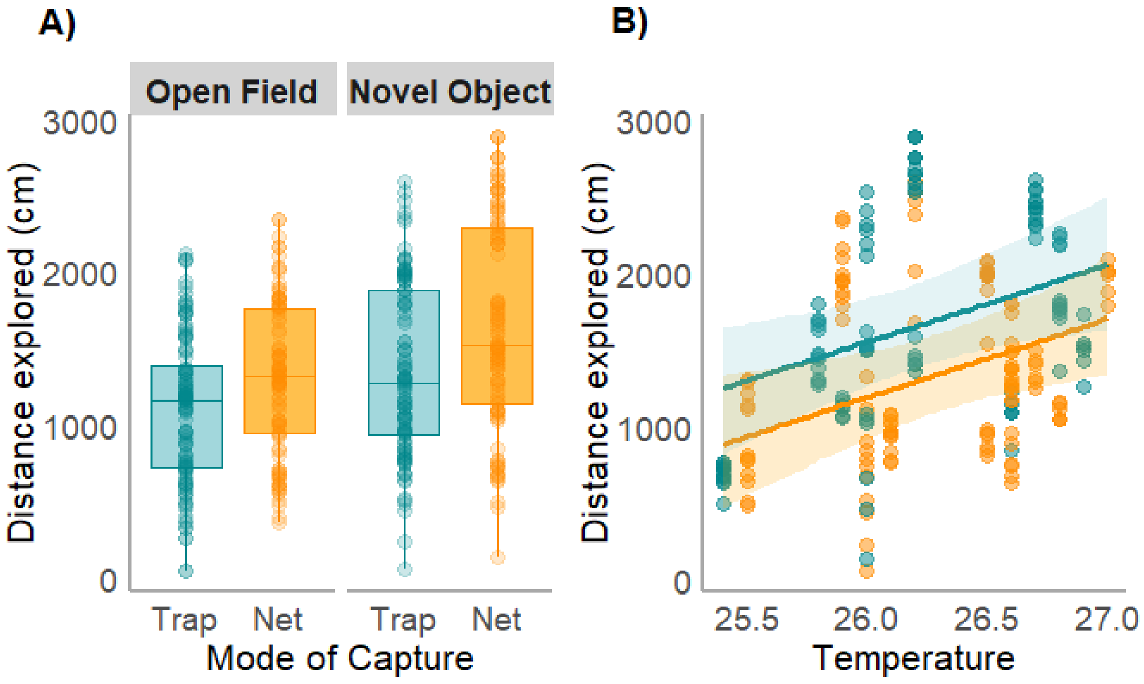

**Figure 3.11)** The effect of experimental and environmental context on exploration: A) Exploration, measured by the total distance covered within a trial, for individuals caught using traps (blue) or nets (orange) in the open field and novel object test. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Each data point represents the distance covered by an individual fish, and data points outside of the range of the whiskers are shown as outliers. B) The relationship between temperature (°C) and exploration. Each data point represents an individual fish. Trend lines represent the predicted values from the linear-mixed effects model, and the shaded regions represent the 95% confidence interval.

There was no evidence that risk-taking differed between fish caught by different gear types. There was no difference in risk-taking, measured as average distance to the centre of the arena, between fish caught using nets or traps (Figure 3.12A; Estimate = 1.10 ± 1.28 SE, df = 66.92, t = 0.86, p = 0.393). There was also no difference in distance to the novel object between gear types (Figure 3.12B; Estimate = 1.55 ± 2.13 SE, df = 33.0, t = 0.73, p = 0.473), and no evidence that temperature influenced risk-taking, either in the open field (Estimate = 1.70 ± 1.03 SE, df = 66.93, t = 1.65, p = 0.103), or novel object test (Estimate = 1.87 ± 2.41, df = 33.0, t = 0.77, p = 0.445).

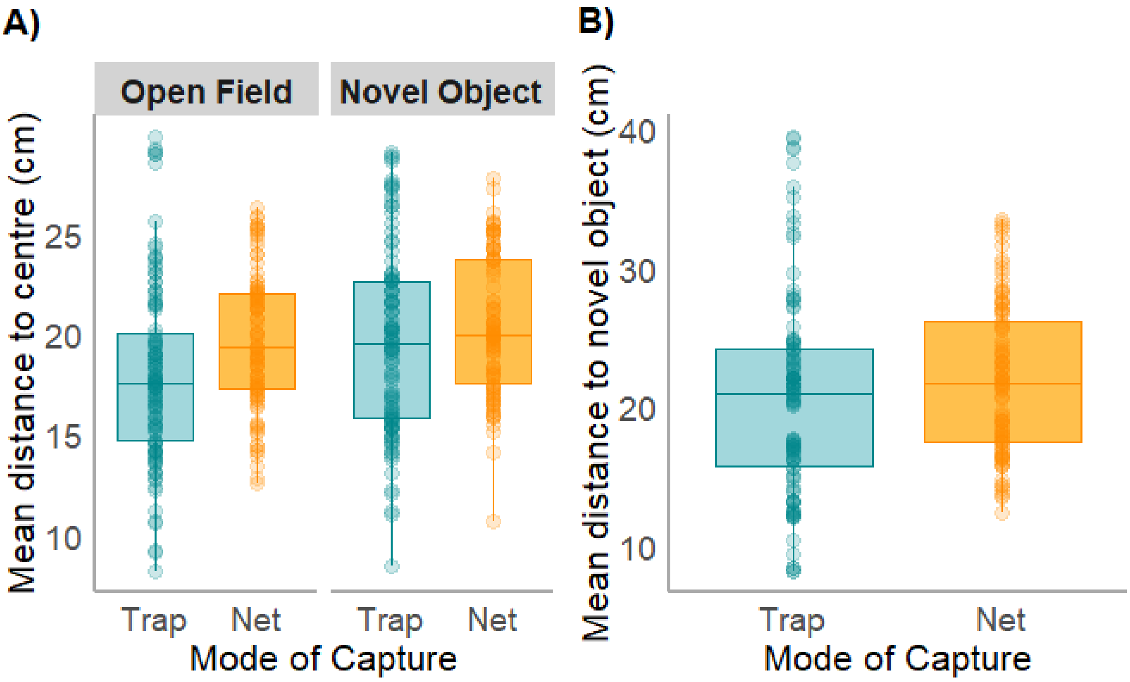

**Figure 3.12)** Risk-taking of fish caught by different gear types. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. A) Risk-taking, measured as the mean distance from a fish to the centre of the arena in open field and novel object tests. Distances closer to the centre indicate higher levels of risk-taking. B) Risk-taking NO, measured as mean distance to the novel object, between fish caught by different gears. Shorter distances indicating higher levels of risk-taking.

## 3.5 DISCUSSION

Understanding how different fishing gears target pre-existing phenotypes is key to uncovering the mechanisms underpinning fisheries selection. While efforts have been made to examine this phenomenon in commercial and recreational fisheries, this study provides the first empirical evidence that fish captured with different artisanal gears in the ornamental fishing trade exhibit distinct behavioural and physiological phenotypes. I hypothesised that cardinal tetra caught by nets, an active gear, would have greater social cohesion and reduced swimming performance, whereas individuals caught by a passive trap would show greater risk-taking and be more exploratory. While I found partial support for my predictions, the findings also highlight an unexpected pattern: behavioural differences were largely influenced by assay choice. Collectively, my findings not only reveal the potential for selection in small-scale fisheries, but more broadly, that decisions made during the experimental design stage can be instrumental to the outcomes of behaviour, which has important implications for the ecological interpretation of behaviour and for the management of harvested populations.

### 3.5.1 Fish Size and Swimming Performance

I found that traps captured larger individuals compared to nets, despite both gears having identical mesh sizes. Size differences between captured individuals in this study are therefore likely to reflect underlying physiological and behavioural traits. For example, larger individuals have higher metabolic demands and a stronger foraging drive, making them more likely to approach and enter a baited trap (Alós et al., 2014). This aligns with my initial hypothesis, as well as previous studies in both commercial and recreational fisheries, where larger individuals are more vulnerable to capture (Allendorf et al., 2008; Kuparinen and Merilä, 2007; Uusi-Heikkilä et al., 2015). In contrast, size-selective harvest has received comparatively little attention in the context of ornamental fisheries. While there is some evidence that ornamental fisheries generally target smaller-bodied individuals due to hobbyist preference (OATA, 2020), virtually no studies have explored how gear type may introduce a size bias, which could have important repercussions for ornamental species that are predominantly caught by traps.

The findings in this chapter also revealed a relationship between gear type and swimming performance. Net-caught fish reached higher maximum swim speeds than trap-caught fish, which was contrary to my initial hypothesis. Typically, passive gears such as traps are considered less selective for traits related to locomotor performance, while active gears such as nets and trawls are more likely to target individuals with poorer swimming ability (Killen et al., 2015; Marras et al., 2010). As my data only included fish that were successfully captured, and not those that escaped, it is possible that individuals with a relatively higher swimming performance were able to escape, which would still mean that those with a poorer swimming performance were targeted. Another possible explanation is that trap-caught fish have behavioural and physiological traits that correlate with lower maximum swimming speeds. For example, as baited traps may be more likely to target fish with higher metabolic demands, the increased feeding motivation may come at a cost to escape capabilities or anaerobic performance. Indeed, previous work has shown that higher levels of activity and metabolic demand are not associated with high burst performance, especially when in novel or constrained environments (Brownscombe et al., 2017; Killen et al., 2012). These findings therefore suggest that gear type has the potential to exert selective pressures on swimming performance, potentially resulting in phenotypic shifts in wild populations of ornamental species.

### 3.5.2 Behavioural Responses Are Context-Dependent

I observed behavioural differences between fish caught using active versus passive gears, however, these differences were context-dependent, influenced by assay type as well as ambient temperature. For example, in the maze test, trap-caught individuals displayed greater risk-taking, with shorter latencies to emerge from the acclimation zone. However, when emergence latency was averaged at the group level, there was no difference in risk-taking between gear types, highlighting how individual variation can be masked in group-level analyses. The difference in behaviour between individuals and groups is important for multiple reasons. On the one hand, it highlights how individual differences in key behavioural traits such as risk-taking could influence group-level dynamics such as collective behaviour in social species (Jolles et al., 2020). On the other hand, it also demonstrates that individuals within a group with greater willingness to take risks are more vulnerable to capture by passive gears, and if risk-prone individuals are consistently caught by traps, this may be selected against. Gear-specific selection on risk-taking, sometimes termed boldness, has been observed in other species, including guppies (*Poecilia reticulata*), where risk-prone individuals were caught by traps faster (Diaz Pauli et al., 2015), and three-spined sticklebacks (*Gasterosteus aculeatus*), where trap-caught individuals emerged from shelter faster (Álvarez-Quintero et al., 2021). In contrast, there were no gear-based differences in risk-taking in the open field or novel object tests, contradicting both the maze test results and prior studies (Álvarez-Quintero et al., 2021).

Group cohesion differed between gear types. Net-caught fish spent more time together in the maze and exhibited lower average neighbour distances in open field and novel object tests, consistent with my hypothesis that net-caught fish are more cohesive. This contrasts with Álvarez-Quintero *et al.* (2021), which found that net-caught stickleback spent a smaller proportion of time with conspecifics. One possible explanation for the difference between findings is that there may be a trade-off between risk-taking and sociability/group cohesion, with individuals that take more risks being more likely to enter traps alone (Kressler et al., 2021; Ward et al., 2004). Another possible explanation in the context of the ornamental industry is that fishers are more likely to detect and net larger groups of fish, rendering gregarious individuals more vulnerable to capture, and therefore selecting against traits that promote social behaviour (Hollins et al., 2018a). Cohesion was also affected by ambient temperature; even small increases in temperature reduced the time individuals spent with conspecifics, regardless of capture method. This aligns with studies showing that temperature can impact social behaviour and cohesion by increasing activity levels (Angiulli et al., 2020; Bartolini et al., 2015; Cooper et al., 2018) or by increasing energetic and foraging demand (Pilakouta et al., 2023). My findings also reveal that cardinal tetra may be sensitive to changes in environmental conditions such as temperature, a finding displayed in other ornamental Amazonian fish species (Kochhann et al., 2015; Ribeiro et al., 2023).

Net-caught fish also exhibited faster maze completion times, which I used as a proxy for exploratory behaviour. There was also a relationship between maze completion time and group cohesion, but this was dependent on gear type. Fish caught by nets completed the maze faster when they spent more time together, suggesting they are able to maintain social cohesion when navigating quickly or that greater group cohesion increased perceived safety, thereby enhancing exploratory behaviour. Additionally, although there were no gear-based differences in exploratory behaviour in the open field and novel object tests, individuals were more exploratory at higher temperatures, further supporting the idea that activity levels and thus vulnerability to capture can vary with environmental context. Indeed, in my study, I found that speed also increased at higher temperatures, suggesting that even small changes in temperature can alter behavioural expression. This is particularly relevant for ornamental species in the Amazon basin, where temperatures are high and fluctuate greatly (Marengo et al., 2018; Val and De Almeida-Val, 1995), having important repercussions for how temperature can modulate behavioural and physiological traits related to capture.

## 3.6 CONCLUSIONS

This study investigated whether different capture methods have different selective effects on the behavioural and physiological traits of a popular aquarium species, the cardinal tetra. Collectively, the results demonstrate that different gears target distinct phenotypes, including body size, swimming performance risk-taking, and cohesion, highlighting the potential for gear-based selection in a fishery that has received little attention in this context. More broadly, the findings also reveal how behavioural outcomes can be shaped by experimental design choices, such as assay type, and environmental factors such as temperature. These context-dependent effects further highlight the complexities involved with interpreting experimental findings to natural populations. By using a suite of assays, I provide a basis for uncovering how ornamental fishing targets specific phenotypes, and how this can contribute to the existing body of knowledge on fishing-induced selection.

# Chapter 4

# Species-specific behaviour and environmental drivers of trap interactions in wild ornamental fishes

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## 4.1 ABSTRACT

The harvest of animals from the wild is a pervasive selective force, especially in fisheries, where harvesting often targets individuals with specific traits. While most research has focussed on large-scale commercial or recreational fisheries, little attention has been paid to artisanal fisheries, particularly those targeting ornamental species. Furthermore, environmental factors such as temperature and oxygen levels influence behaviour of fishes, such as boldness and sociability, but their role in the harvesting process remains poorly understood. Here, I used underwater video to examine how two ornamental Amazonian fishes, *Hemigrammus spp.* and *Copella nattereri*, interact with artisanal trap gear. I quantified the number of passes, inspections, entries, and exits using latency to inspect and enter traps as proxies for boldness, and coefficients of dispersion (CD) to assess sociability and group coordination. I found that the majority of fish that inspected traps did not enter them, and a given trap typically caught one species over the other. Overall, *Copella* were captured more frequently, but within individual trials there was no statistical difference in catch numbers between species. While both species inspected traps, *Hemigrammus* exhibited significantly more passes and a higher rate of inspection. Latency to inspect and enter traps did not differ between species but decreased with increasing temperature for both. *Hemigrammus* also displayed greater group coordination, with higher CD values across behaviours. Notably, temperature had opposing effects on coordination: for *Hemigrammus*, CD of inspections increased with temperature and CD of exits decreased, whereas for *Copella*, inspection CD decreased and exit CD increased. These findings reveal that different species interact with fishing gear in behaviourally distinct ways, influenced by environmental conditions. This highlights the potential for selective pressures to vary not only by species, but also with ecological context. Understanding such dynamics is critical for predicting how artisanal fisheries may shape behavioural traits in wild populations.

## 4.2 INTRODUCTION

The harvest of animals from the wild is a major selective force that can have important repercussions for evolution (Allendorf et al., 2008; Allendorf and Hard, 2009; Darimont et al., 2015, 2009). From trophy hunting to harvesting for subsistence and population control, the capture of animals by humans has led to both direct and indirect selection in wild populations (Leclerc et al., 2017; Miller, 1957; Mysterud, 2011; Pigeon et al., 2016). Harvest-associated selection has been particularly well-documented in commercial fisheries, particularly the impacts of increased mortality and non-random removal of specific phenotypes including those related to size and life-history traits (Enberg et al., 2012; Heino et al., 2015). If the traits targeted by fisheries are heritable, this can lead to a phenomenon known as fisheries-induced evolution (FIE) (Crespel et al., 2021a; Heino et al., 2015, 2013). While the focus on FIE has largely been on size and maturation related traits (Enberg et al., 2012), there is now increasing evidence that behavioural traits can also be targets of selection, with individuals that are bolder or more sociable being removed from a population by recreational and commercial fisheries and being selected against (Arlinghaus et al., 2017; Diaz Pauli et al., 2015; Hollins et al., 2019; Koeck et al., 2020). However, the mechanisms behind how or why specific behaviours are selected are currently not understood.

The methods used to capture fish can also be selective, as different gear types tend to capture individuals with specific traits (Álvarez-Quintero et al., 2021; Hollins et al., 2018). Active gear types such as trawls target groups of fish and are more likely to capture social species that have a higher tendency to shoal, or social individuals that follow a leader into a trawl (Hollins et al., 2018). In contrast, passive gears such as traps rely on individuals encountering and voluntarily interacting with a gear. The behaviour of fish around traps has been well-documented in commercial food fisheries (Thomsen et al., 2010; Winger et al., 2016). Baited traps capture individuals with greater food searching behaviour (Thomsen et al., 2010), which is often linked to a higher metabolic demand (Killen et al., 2011). Similarly, passive gears have been shown to attract bolder individuals (Arlinghaus et al., 2017; Biro and Dingemanse, 2008; Diaz Pauli et al., 2015; Wilson et al., 1993), although how this relates to capture is less understood. For example, bolder fish may encourage other social individuals to enter a trap (Hollins et al., 2018), whilst more aggressive or territorial individuals may guard the entrance of a trap or deter others (Finucci et al., 2019; Winger et al., 2016), indicating the importance of recognising differences in behaviour within and between species. Abiotic factors such as light (Hedgärde et al., 2016), current (Folkins et al., 2021), temperature (Hollins et al., 2021; Thomsen et al., 2010), and hypoxia (Thambithurai et al., 2019) further affect behaviour during the capture process. Elevated temperature increases activity, which can lead to more encounters with gear. Increasing temperature also influences metabolic rate (Biro and Stamps, 2010), leading to a greater food demand (Killen et al., 2011), as well as an increase in boldness that can increase the likelihood of finding and entering a gear (Winger et al., 2016). Conversely, hypoxia can reduce appetite and lead to a reduction in foraging behaviour (Chabot and Claireaux, 2008; Killen et al., 2012), which could lead to a decrease in gear encounter rates. Furthermore, while the behaviour of fish around commercial traps and trawls is well observed, this knowledge is absent for many smaller scale artisanal fisheries.

The ornamental fishing industry is a multi-billion dollar industry that involves the collection and distribution of fishes for the aquarium industry across the globe (Ojelade et al., 2024; Saxby et al., 2010). The trade is estimated to handle up to 1.5 billion individual fish per year (Evers et al., 2019; Stevens et al., 2017) including 4,500 freshwater species (Miller-Morgan, Tim, 2009), although estimates vary widely for the number of individuals collected and transported and the consequent profits made (Evers et al., 2019; King, 2019; Stevens et al., 2017). It is also estimated that 10% of freshwater fishes used in the ornamental trade are harvested from the wild (Evers et al., 2019; OATA, 2016). The state of Amazonas, in Brazil, is often used as a case study for the capture of wild-caught ornamental fishes (Evers et al., 2019; OATA, 2016; Tribuzy-Neto et al., 2021; Zehev et al., 2015) with the trade contributing up to 80% of the local economy and supporting livelihoods (Tribuzy-Neto et al., 2021; Zehev et al., 2015). A large variety of Amazonian species are caught using artisanal gears including *cacurí*; a passive, non-destructive trap designed to catch fish alive (Phang et al., 2019). While *cacurí* offer less precision when targeting commercially important species, they are typically favoured for their low environmental impact, affordability, and suitability for capturing small bodied species, particularly in areas that are harder to access (Ferreira and Yamamoto, 2017; Ladislau et al., 2020; Phang et al., 2019). However, little is known about how specific species behave around *cacurís*, or how environmental factors such as water temperature and dissolved oxygen, which both fluctuate widely in Amazonian ecosystems (Marengo et al., 2018; Val and De Almeida-Val, 1995), influence capture dynamics. These environmental variables are known to affect behavioural traits such as sociability and boldness (Pineda et al., 2020; Tiddy et al., 2024), which may in turn mediate vulnerability to capture.

Despite the ecological and economic significance of the ornamental trade, the behaviour of ornamental species in the wild has rarely been studied, particularly in the context of selective harvest. In this study, I focus on two abundant Amazonian species, *Copella nattereri* and *Hemigrammus spp.*, which are commonly found schooling in shallow floodplain habitats and frequently caught by artisanal fishers (Tribuzy-Neto et al., 2021). Although they are not the most valuable targets for ornamental fishers, they are still amongst the most commonly exported (Tribuzy-Neto et al., 2021). Additionally, their schooling behaviour, abundance, and accessibility make them suitable for behavioural observation and analysis of species-specific responses to fishing gear. While both species have a similar temperature tolerance (Beltrão Dos Anjos et al., 2017; Fróis et al., 2021), they both inhabit similarly oxygen and temperature-variable environments. This variation can also have important implications for selection as trait variation and heritability changes across environments, potentially amplifying or weakening harvest-associated selection (Thambithurai et al., 2019). Additionally, given the rapid generation times of these small Amazonian species, they represent a valuable model for investigating how selection can operate in wild populations (Gordon et al., 2015).

By capturing underwater footage of Amazonian fishes during the trapping process, I provide a low-cost method for observing behaviours of individuals in the wild. I also examine differences between species in their interactions with a passive gear type, including decisions to inspect, as well as decisions to bypass, a behaviour usually not examined by fisheries simulations (Hollins et al., 2019; Thambithurai et al., 2022, 2018). By linking this with environmental data, I examine the impacts of abiotic factors that affect behaviour, such as temperature and dissolved oxygen levels (Pineda et al., 2020; Tiddy et al., 2024).

Specifically, I aimed to address the following questions: 1) what behavioural patterns and processes underlie the likelihood of fish being captured when in proximity to a trap; 2) is there a difference between species in the behaviours observed; and 3) do environmental factors influence the behaviours of individuals around a trap?

## 4.3 METHODS

### 4.3.1 Sampling Area

Fieldwork was conducted within the Puranga da Conquista Sustainable Development Reserve (SDR) in the Brazilian Amazon. The SDR was created in 2014 in the Rio Negro Basin and is made up of approximately 77,000 hectares with 15 communities living within the protected area (Instituto Socioambiental, n.d.). Here, fishing is only permitted for subsistence for members of the community or for researchers with a permit and there is no history of fishing for the aquarium trade. Fishing occurred during the dry season, which is when ornamental fishers catch fish for the ornamental trade (da Silva Ladislau et al., 2021). In the dry season, floodplains dry into smaller streams known as igarapés and the capture of fishes becomes easier in these smaller streams. Fishing took place at three field sites from 15-19 September 2022 (Figure 4.1, Supplementary Table 4.1).

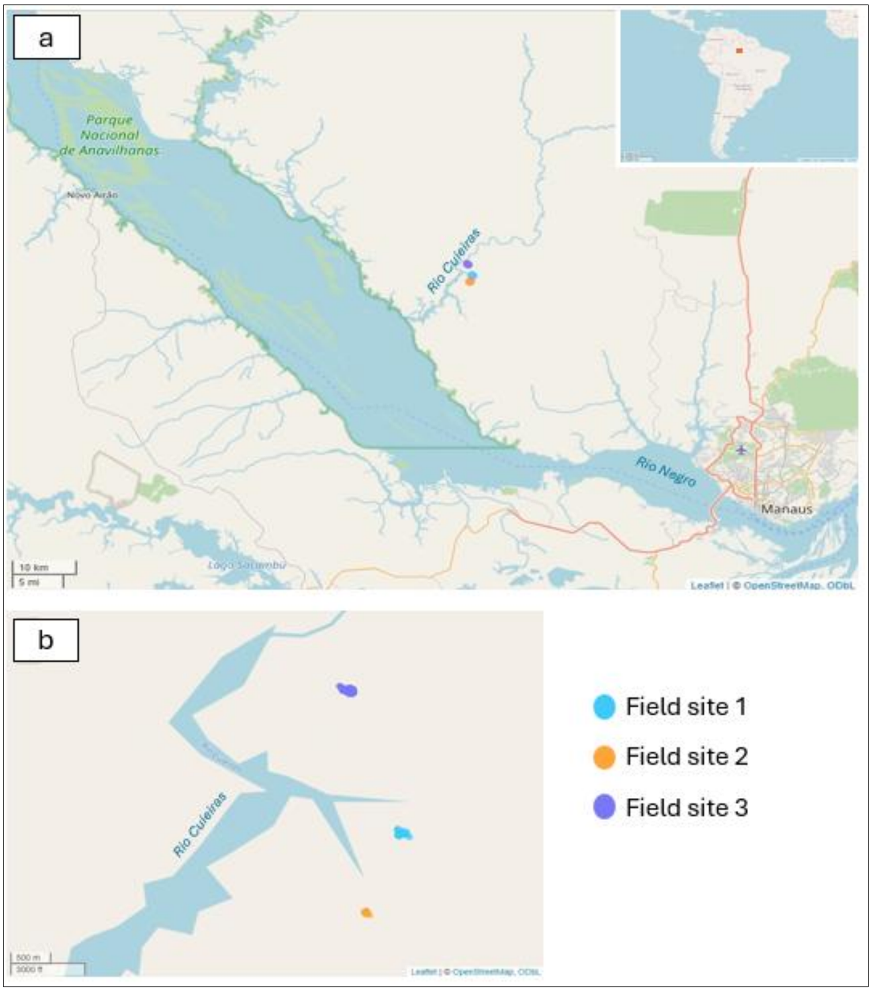

**Figure 4.1)** Map of field sites used for fishing: a) area showing landmarks such as Manaus and the Rio Negro as well as an inset map of its location within Brazil; b) area zoomed in to show where surveying took place within the three different field sites along igarapes of the Rio Cuieiras. The shape of the tracks corresponds to live data of our movements within the site. Maps were made using downloaded gpx data visualised with the leaflet package in R (Cheng et al., 2024).

### 4.3.2 Sampling Method

Fish were caught using an artisanal trap known as a *cacurí* (Figure 4.2). Traps were placed by experimenters within a field site and were placed so that the top of the trap emerged from the surface of the water, with water depth varying between sites and the traps were baited with rice or manioc powder. The process for capture was guided by a partner fisher and the trapping process closely mimicked that of the ornamental fishing trade.

**Figure 4.2)** *Cacurí* used for trapping fish consisting of a metal frame (43 cm H, 22 cm diameter) covered in netting (<1.5 mm mesh size) attached to a wooden base with an inverted funnel entrance (6 cm diameter). Photo by M. Pineda.

Each day, traps were placed within a field site 6-14 times resulting in 42 trapping trials across the five days and three sites. Traps were placed in pairs, with the distance between traps varying according to environmental constraints. To reduce the likelihood of behavioural interference, traps were typically positioned 10 meters apart and trap locations were not reused across trials. The studied species were trapped outside of the breeding season so were not considered to be territorial, reducing the risk of interference. Cameras (GoPro Hero 4, Paralenz) were opportunistically placed at the entrance of traps to record the capture process, collecting footage for 36/42 trials. The cameras were operated manually by starting videos when they were placed into position. The videos then lasted 30 minutes. Environmental data (Supplementary, Figures 4.1-4.2: water temperature, air temperature, pH, oxygen saturation (% and mg/l) was also collected at each trap location using a YSI meter (YSI Pro20) as well as time of day (date and time). The experimental procedures were approved by the Animal Use Ethics Committee of the Brazilian National Institute for Research of the Amazon (CEUA-INPA), number 01280.000209/2018-74. The permit for the collection of the biological material to carry out the research was authorized by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA/SISBIO), number 29837-13.

### 4.3.3 Video Analysis

Video analysis was done manually using Solomon Coder (version 19.08.02), which allows for the coding of behavioural events across the duration of a trial. The videos featured two of the most abundant species in the area, *Copella nattereri* and *Hemigrammus* spp., hereby referred to as *Copella* and *Hemigrammus*, respectively, which are both social schooling species. Two distinct forms of *Hemigrammus* were observed in the videos, although species-level identification was not possible. These forms were visually distinguishable and are referred to here as *Hemigrammus sp. 1* and *Hemigrammus sp. 2*. *Hemigrammus sp. 1* was the most abundant form and had a red coloration in the upper region of the eye and a clearly marked lateral line. *Hemigrammus sp. 2* exhibited a smaller red area around the eye and a large black spot on the caudal peduncle. Behavioural analysis was conducted using *Hemigrammus sp. 1* only, while *sp. 2* is included in the taxonomic list (Supplementary Table 4.2).

Videos were categorised into visibility type -high, medium, or low- to establish a criterion for determining suitability for behavioural analysis. The classification was based on the quality of the recording and how much of the trap was visible in each recording: high visibility videos showed the entirety of the trap, medium visibility videos showed a portion of the trap, and low visibility videos were largely obstructed or poorly lit (Figures 4.3A-C). Low visibility videos typically lacked sufficient light or clarity to reliably identify species or code fish behaviours and were therefore excluded from behavioural analysis to preserve data quality. This resulted in 9 high, 13 medium, 14 low videos.

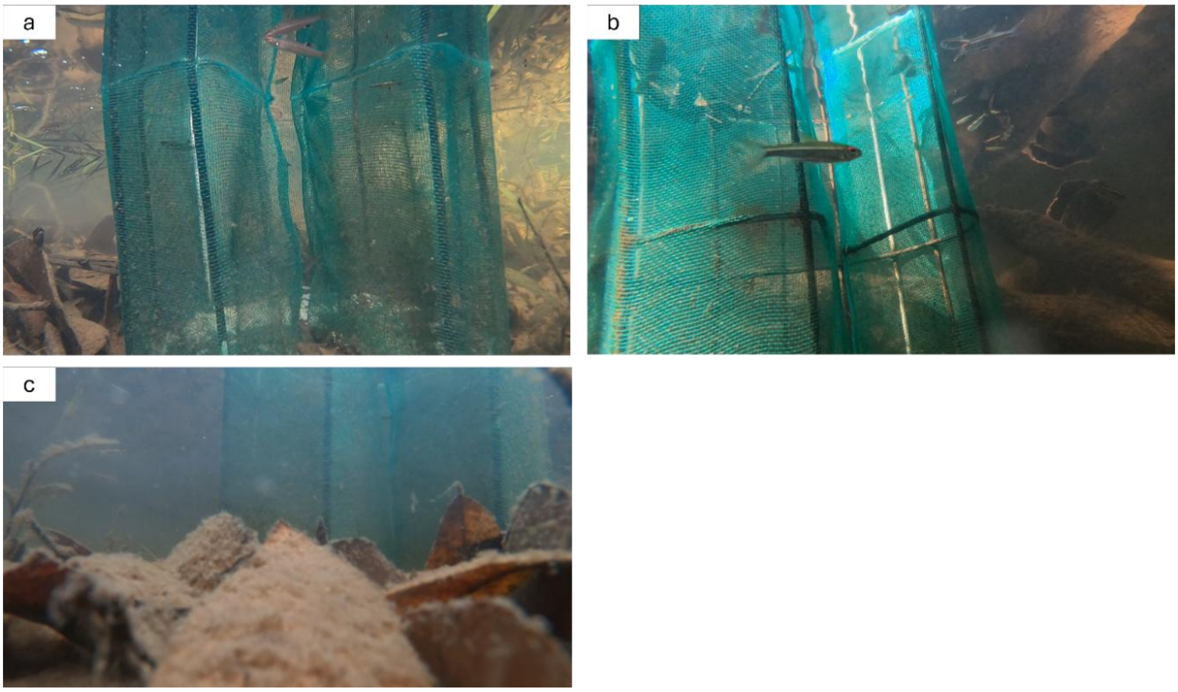

**Figure 4.3** Visibility classifications for trap videos: A) high visibility- entire trap can be seen from top to bottom; B) medium visibility- the top of the trap can be seen but not the bottom; C) low visibility- both top and bottom of trap cannot be seen, and view is partially obscured by leaves and sediment.

The number of passes, inspections, entries, and exits was recorded for each species at each trap as well as the time each behaviour happened in the video. Descriptions for each behaviour are shown in table 4.1.

**Table 4.1)** Description of each behaviour and how it was classified.

| **Behavioural Measure** | **Description** |
|---|---|
| Pass | Whenever an individual passes by any visible part of the trap without inspecting it |
| Inspect | Whenever an individual approaches the trap, touches the trap, or interacts with any fish on the inside of the trap either at the entrance or any other visible part of the trap |
| Enter | Whenever an individual enters the trap completely |
| Exit | Whenever an individual exits the trap completely |
| Latency to inspect | Time taken until the first fish of each species inspects the trap (seconds) |
| Latency to enter | Time taken until the first fish of each species enters the trap (seconds) |
| Rate of inspection | Rate of inspection within each trial for each species calculated within a specific time interval. Later averaged per trial for modelling. |
| Rate of entry | Rate of entry within each trial for each species calculated within a specific time interval. Later averaged per trial for modelling. |
| Sociability | Whether or not behaviours are clustered in time |

The location in which fish entered the trap was also recorded and was classified as either top, middle or bottom relative to the surface of the water column. Analysis was completed for all high visibility videos first. Preliminary analysis found that most individuals entered near the top of the trap (Supplementary Figure 4.3). Subsequently, medium visibility videos were then analysed if the top of the trap was visible. Videos that were classified as low visibility were not used for video analysis or subsequent statistical analysis. Any videos that were less than 30 minutes long were also discarded. This resulted in 18 30-minute videos used overall for video and statistical analysis.

Further behaviours were then analysed manually. The latency of the first individual of each species to inspect and enter the trap was used as a proxy for boldness, with bolder individuals inspecting or entering the trap sooner. The number of individuals of each species retained by a trap at the end of the trial was calculated by subtracting the number of exits from the number of entries. The rate of inspection and rate of entry of each species was also calculated within each trial by dividing the time in the 30-minutes videos into 60-second time intervals. The number of behavioural events (either inspections or entries) were recorded within the interval to provide a behavioural count. The rate of the behaviour (inspection or entry) was then calculated as: Rate of Behaviour = Behavioural Count / 60, to convert the raw count of inspections into a rate of behaviour per second.

The sociability of each species was then analysed by calculating the coefficient of dispersion (CD) for each behaviour in the 30-minute trial (Chapman and Chapman, 1994; Hollins et al., 2019; Killen et al., 2018; Pineda et al., 2020). Each trial was split into 10-second intervals and the number of behaviours within each time bin were counted. CD was then calculated as the variance/mean ratio across the intervals, with CD ≈ 1 indicating events were randomly distributed, CD < 1 indicating events were evenly spread, and CD >1 indicating a clustering of events.

### 4.3.4 Statistical Analyses

All statistical analyses were carried out using R version 4.2.2 (R Core Team, 2022). Linear models were used to test the effects of species, site, date, and environment on the behaviours observed in the 42 trapping trials. The response variables were the frequency of passes, inspections, entries and exits, the number of individuals captured, inspection latency, entry latency, sociability, average rate of inspection, average rate of entry, and the coefficient of dispersion of each behaviour. For all models, the explanatory variables were species, site, date, water temperature, oxygen saturation as well as all relevant two-way interactions. Initial models included any main predictors that were not correlated, and model selection occurred via a stepwise approach based on Akaike Information Criterion (AIC) values using the MASS package (Ripley and Venables, 2009). The final model was selected when no further improvement in AIC could be made. In the results section, P-values are described as suggested by Muff et al., (2022), which classifies significance thresholds as ‘little to no evidence’ ($P > 0.1$), ‘weak evidence’ ($0.05 < P < 0.1$), ‘moderate evidence’ ($0.01 < P < 0.05$), ‘strong evidence’ ($0.001 < P < 0.01$), and ‘very strong evidence’ ($P < 0.001$).

## 4.4 RESULTS

### 4.4.1 Number of Fish Captured

Overall, while more captures were observed for *Copella* compared to *Hemigrammus* across trials (Figure 4.4A), there was no statistical evidence to support a difference in the number of individuals captured between species within a trial (Figure 4.4B). There was weak evidence to suggest that date of capture influences the number of individuals caught within a trial (Supplementary Table 4.3; $t = -1.725$, $p = 0.095$). However, comparing the number of individuals captured from each species within a trial revealed that, within a given trial, one species would often be caught in a greater amount than the other, i.e. more *Copella* and fewer *Hemigrammus*, or vice versa (Figure 4.4C).

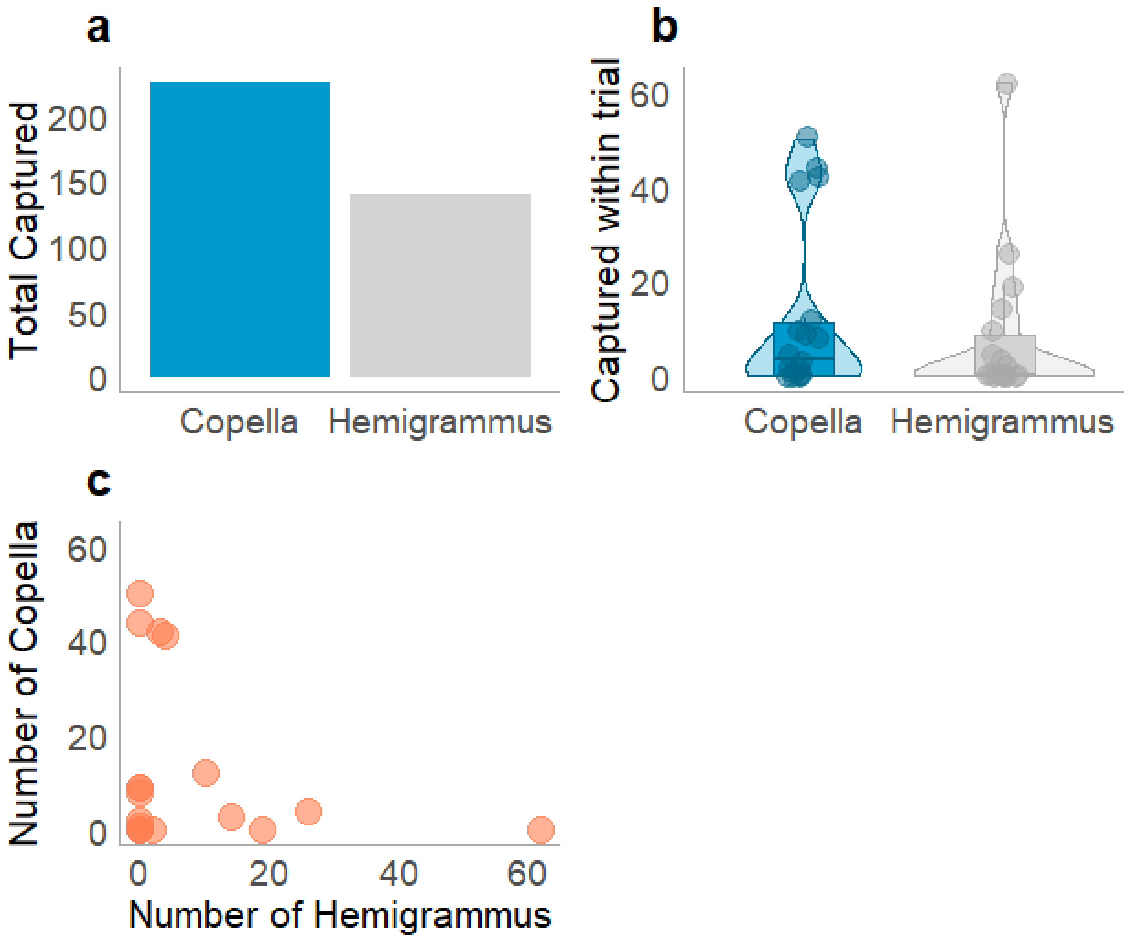

**Figure 4.4)** Number of fish captured by traps: A) total number of individuals captured of each species across the field season; B) total number of individuals captured of each species within each trial - here, each data point represents a trial; C) the relationship between the number of individuals of each species caught within a trial.

### 4.4.2 Frequency of Behaviours

Over 5,000 behavioural events were coded during video analysis. Overall, the number of passes and inspections were greater than the number of entries and exits for both species (Figure 4.5). Furthermore, there was a difference in the total number of inspections leading to entries between species ($t = 5.252$, $p < 0.001$), with 34.5% of inspections resulting in entries for *Copella* and only 9.3% of inspections resulting in entries for *Hemigrammus*. Furthermore, 27.6% of *Copella* that entered a trap exited, as did 22.7% of *Hemigrammus*.

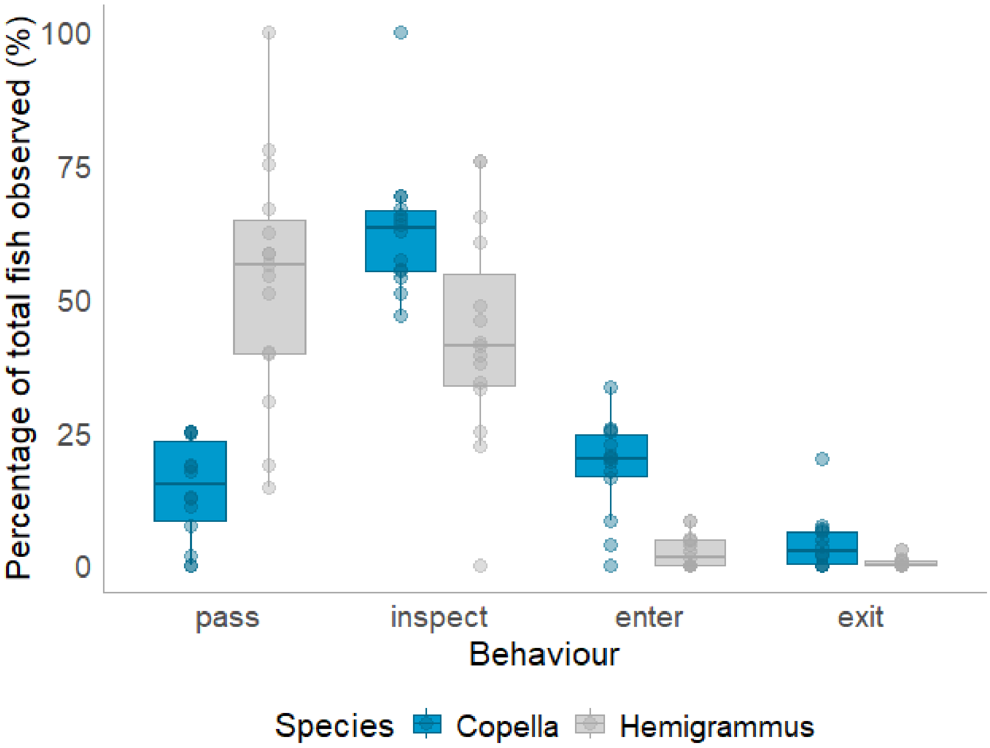

**Figure 4.5)** The number of passes, inspections, entries and exits observed as a percentage of total behaviours. Each data point representing an individual trial.

While there was strong evidence that both date of capture (t = -2.151, p = 0.04) and species (t= 3.821, p<0.001) explained variation in the number of observed passes, there was weak evidence for date and species explaining variation in the number of inspections, entries, and exits (Supplementary Figure 4.4; Supplementary Table 4.3).

### 4.4.3 Inspection and Entry Latency

While the median inspection latency was lower for *Hemigrammus* compared to *Copella*, there was no evidence to suggest an overall difference between species in the latency of inspections (two sample t test: t = 1.289, p = 0.210) nor entries (two sample t test= t = 0.048, p = 0.963) due to the large amount of within-species variation (Figure 4.6; Supplementary Table 4.4).

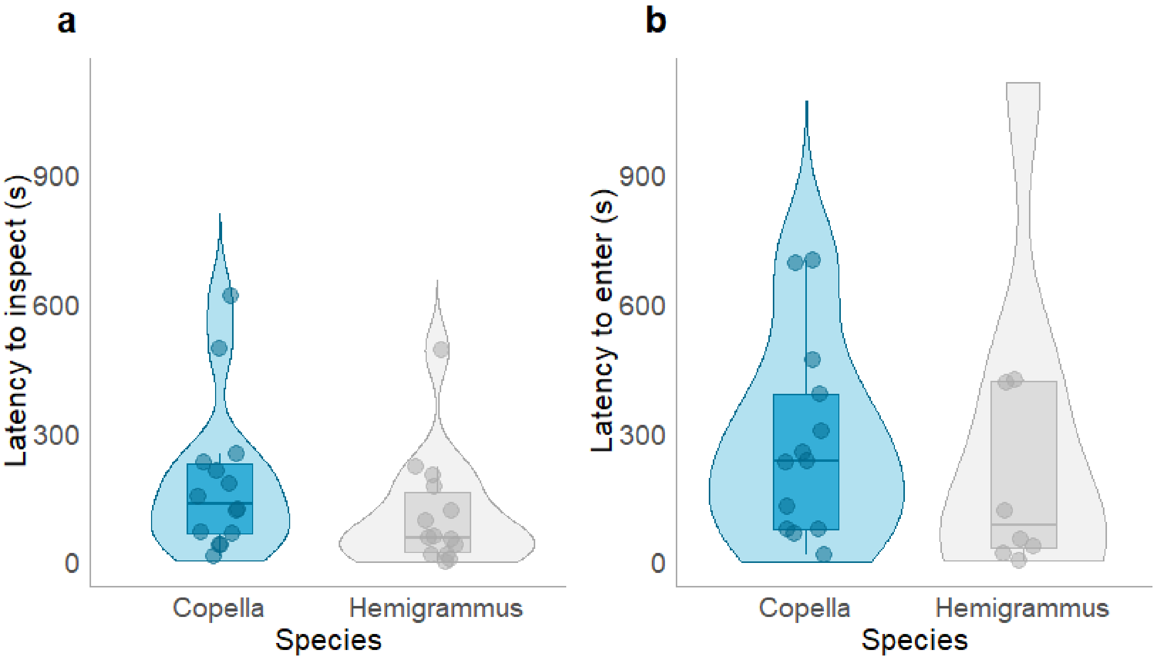

**Figure 4.6)** Inspection and entry boldness of *Copella* and *Hemigrammus*. Each individual data point corresponds to the first individual to inspect or enter within a trial: A) time taken for the first individual within a trial to inspect a trap; B) time taken for the first individual within a trial to enter a trap.

There was strong evidence that inspection latency decreased at higher temperatures (Figure 4.7A; t= -2.969, p = 0.006). Furthermore, while there did appear to be an interaction between water temperature and species, there was no statistical evidence for this (t = -0.816, p = 0.425). Additionally, there was a moderate negative correlation between inspection latency and the number of individuals caught within a given trap, as traps with shorter inspection latencies captured more individuals (Figure 4.7B; Pearson: r = -0.384, p = 0.044). Similarly, there was also a negative correlation between latency to enter a trap and the number of individuals caught by a trap (Figure 4.7C; Pearson: r = -0.429, p = 0.05).

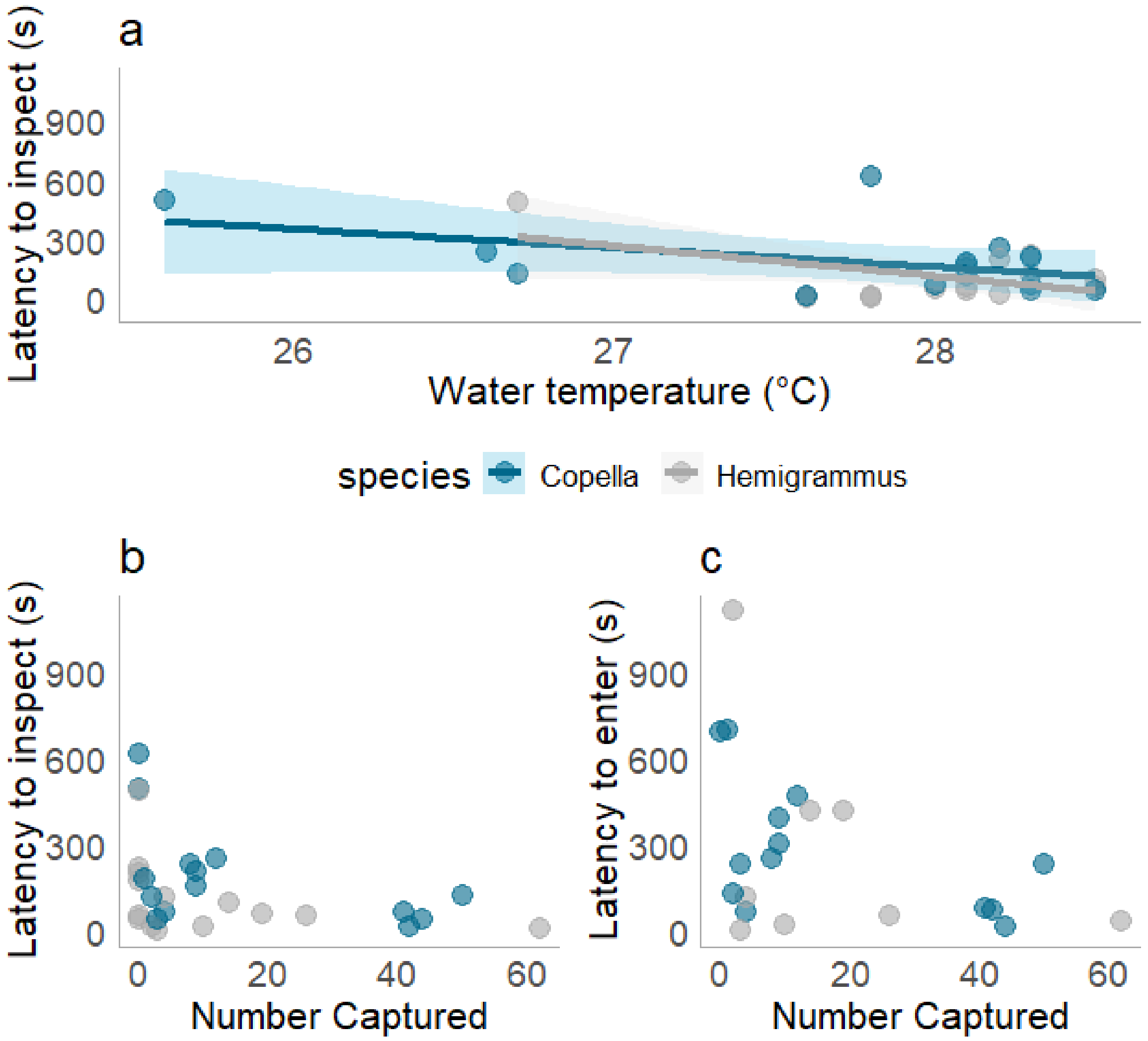

**Figure 4.7)** Factors affecting latency to inspect and enter a trap: a) the relationship between latency to inspect and water temperature; b) the time taken for the first individual to inspect a trap against the number of individuals captured; c) the time taken for the first individual to enter a trap against the number of individuals captured. Each data point represents an individual trial, and each data point is coloured according to species.

### 4.4.4 Inspection and Entry Rate

Inspection rate differed within and across trials (Figure 4.8). Inspections were observed in 17 of the 18 trials that were used for video analysis. Five trials had inspections for only one species while the remaining trials had inspections for both. Within trials, the rate of inspection over time varied. While some trials had a peak in activity at the start, other trials had a peak towards the end of the trapping period, and others had a continuous rate of activity. This pattern also differed across trials and the rate of inspection also differed between species across trials. However, the level of activity within a trial was usually not high for both species simultaneously, with one species tending to have a greater level of activity over the other.

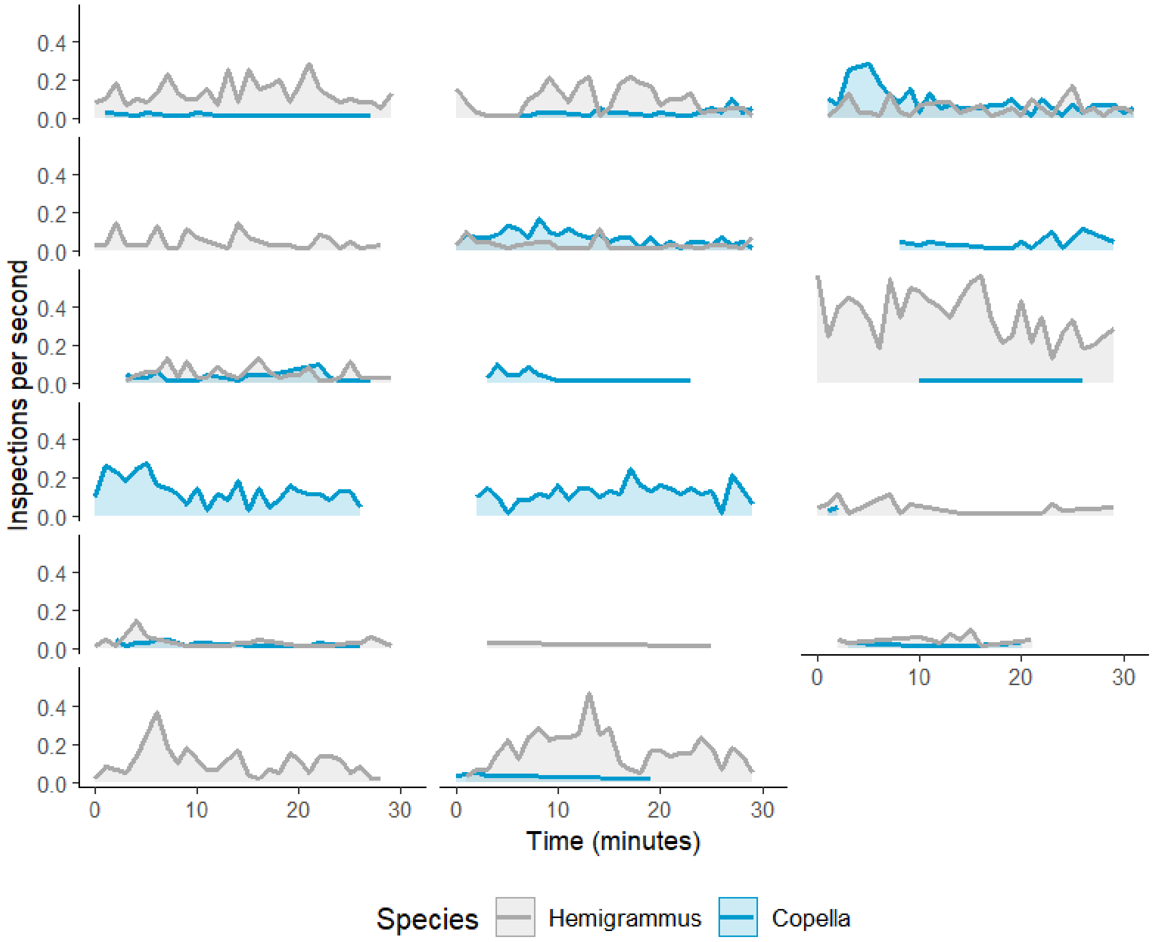

**Figure 4.8)** The rate of inspection of a trap over a 30-minute trial. Each panel represents an individual trial, with each line displaying the peaks and troughs in the rate of inspection over the entire trial. The y- axis represents the inspections per seconds and the x-axis represents the time within the 30-minute trial. The colour of the line corresponds to the species.

Inspection rate was affected by several factors. For example, there is strong evidence that both date of capture (Figure 4.9C; t = 3.064, p = 0.006) and species (Figure 4.9A; t = 2.450, p = 0.023) can explain variation in the rate of inspection, with higher rates of inspection for *Hemigrammus* (Supplementary Table 4.5). There was also moderate evidence that dissolved oxygen influenced the inspection rate, with higher rates of inspection at higher dissolved oxygen concentrations (Figure 4.9B; t = 2.505, p = 0.021). Additionally, there was a positive correlation between the number of individuals caught within a trap and the rate of inspection (Pearson: r = 0.668, p <0.001).

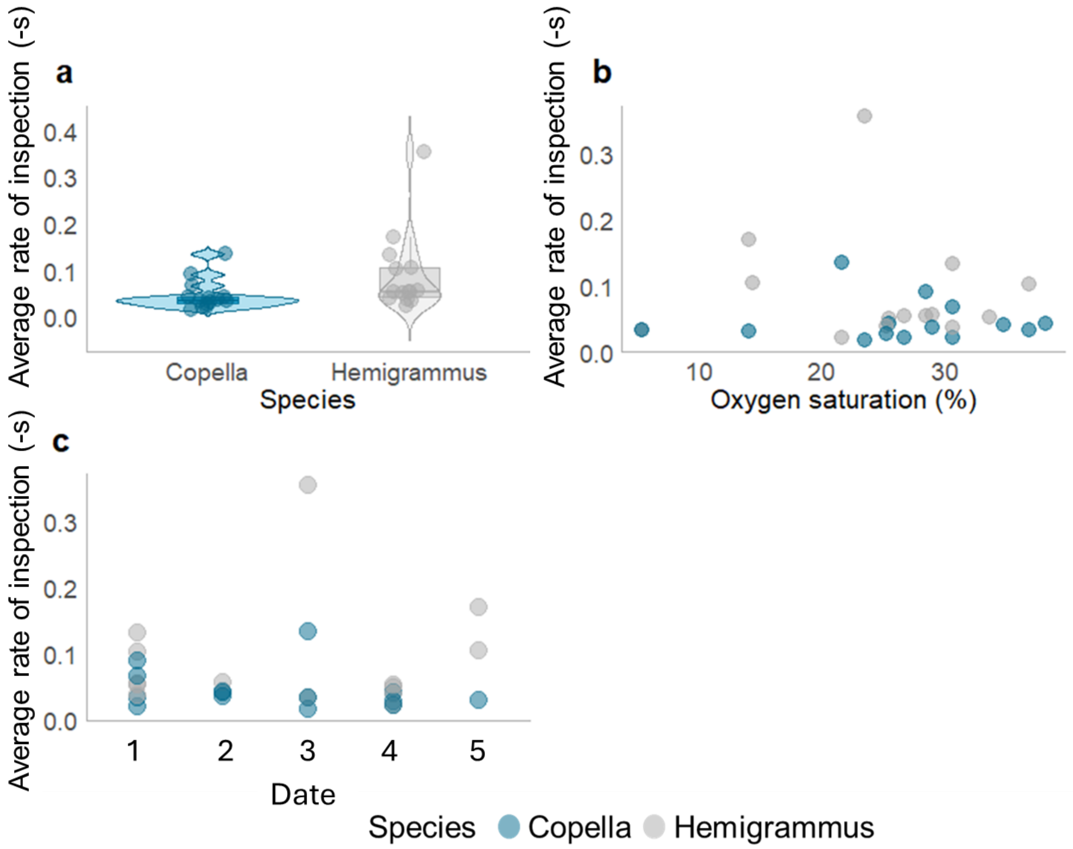

**Figure 4.9)** The impact of predictor variables on the average rate of inspection: A) the difference in the rate of inspection between species; B) the relationship between rate of inspection and oxygen saturation; C) the average rate of inspection across trapping dates. As dates were successive between the 15th-19th of September, these are represented by a number between 1-5 for simplicity. For all plots, each data point represents the average rate of inspection within a trial.

The entry rate also differed across and within trials. Entries were observed in 16 of the 18 and 68.8% of the trials had entries for only one species. Within trials, the entry rate also differed, with some trials having peaks of entries at the start of the trial and others having peaks of activity occurring throughout the duration of the trial (Figure 4.10). Furthermore, while variation in the entry rate could be explained by date of capture ($t = 4.145$, $p < 0.001$), there was little evidence that any of the other predictor variables had an impact on the entry rate (Supplementary Table 4.5). However, there was a strong positive correlation between the rate of entry and the number of individuals caught by a trap (Pearson: $r = 0.888$, $p < 0.001$).

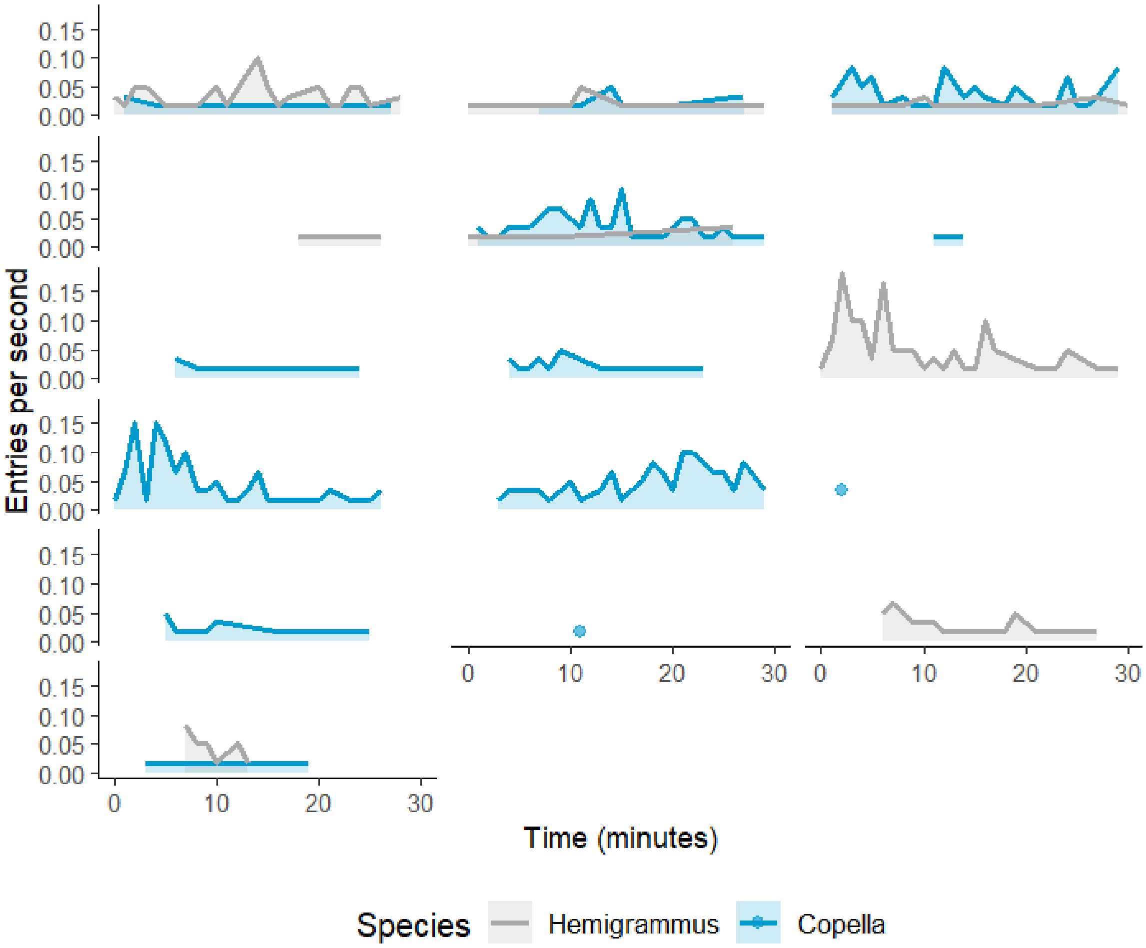

**Figure 4.10)** The rate of entry of a trap over a 30-minute trial. Each panel represents an individual trial, with each line displaying the peaks and troughs in the rate of entry over the 30-minute trial. Panels with a single data point indicate that only one entry occurred. The y- axis represents the entries per seconds and the x-axis represents the time within the 30-minute trial. The colour of the line corresponds to the species.

### 4.4.5 Sociability

Clustering in the timing of behavioural events was found in only six trials (Figure 4.11). When synchronised behaviours did occur, it was only for passes and inspections. There was also evidence overall for a difference in the coefficient of dispersion (CD) between behaviours, with CD declining between behaviours (from pass to entry). There was also evidence for differences in CD between species, with *Hemigrammus* having a higher coefficient of dispersion for all behaviours (Figure 4.11; Supplementary Table 4.6).

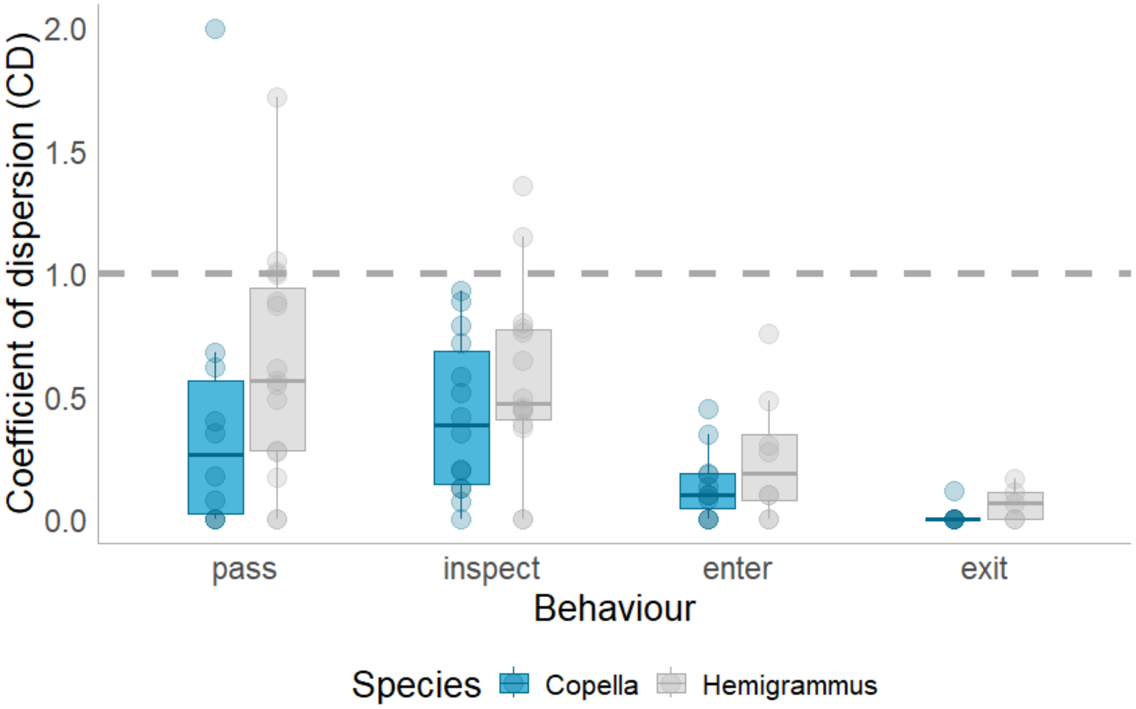

**Figure 4.11)** The coefficient of dispersion of four behaviours (passes, inspections, entries, and exits) for each trial and for both species.

Several factors influenced the degree to which behaviours were temporally clustered. For passes, there was moderate evidence that date of capture influenced CD (Figure 4.12A; t = 2.365, p = 0.034). Additionally, there was moderate evidence that water temperature influenced the CD of inspections (t = 2.309, p = 0.032). However, this was dependent on species, with greater CDs at higher temperatures for *Hemigrammus*, but the opposite trend for *Copella* (Figure 4.12B). Similarly, the effect of water temperature on CD for exits varied between species (Supplementary Table 4.6), with higher CDs at elevated temperatures for *Copella* rather than *Hemigrammus* (Figure 4.12D; t = 4.657, p = 0.01). Finally, there was no evidence that any of the predictor variables apart from species (Supplementary Table 4.6) had any impact on entry CD (Figure 4.12C, t= 2.215, p = 0.049).

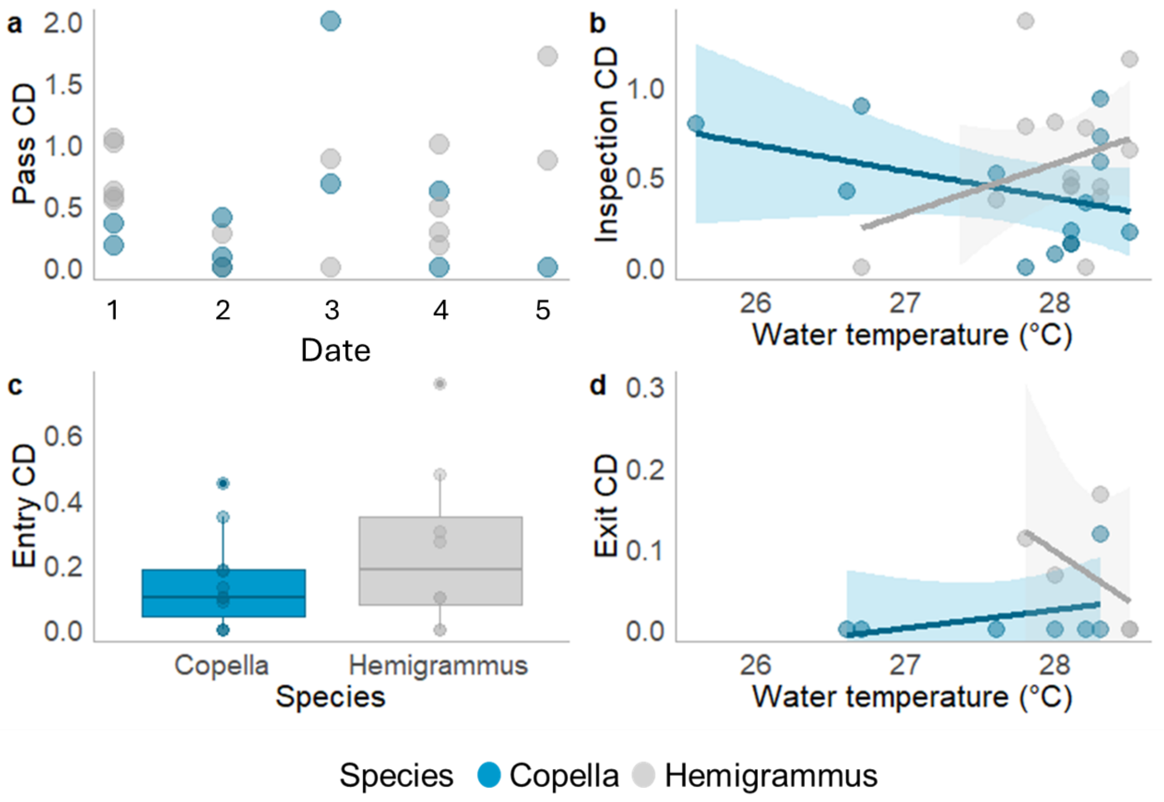

**Figure 4.12)** The impact of model predictors on the coefficient of dispersion (CD) of four behaviours (passes, inspections, entries, and exits) for both species. Each data point represents the overall CD for a given behaviour within a trial: A) the impact of date of capture on the CD of passes. As dates were successive between the 15th-19th of September, these are represented by a number between 1-5 for simplicity; B) the impact of water temperature on the CD of inspections; C) the impact of location on the CD of entries; and D) the impact of water temperature on the CD of exits.

## 4.5 DISCUSSION

Understanding the relationship between an individual's traits and its susceptibility to capture is crucial for unravelling the mechanisms through which interactions with fishing gears can lead to changes in a targeted population (Hollins et al., 2018). The capture process involves many steps, and identifying behavioural mechanisms underlying capture is essential to determine which traits are under selective pressure from fisheries (Ward and Webster, 2016). Furthermore, as physiological and behavioural traits related to capture are also closely linked with environmental factors (Hollins et al., 2018), it is important to understand how changes in environment can modulate behavioural responses to gears. Here, I demonstrate that observations of traps in the wild provide insights not only into the number of individuals caught, an endpoint often focussed on by previous studies (Hollins et al., 2019; Thambithurai et al., 2022, 2018), but also into pre-capture behaviours, such as passes and inspections. While this study did not directly measure phenotypic traits outside of the capture process, insights into behavioural decision-making shed light on which behaviours influence capture, and which do not. Additionally, I reveal how environmental factors, such as temperature and dissolved oxygen, influence how individuals approach and exit traps, and how the relationship between behaviour and environment can differ between species.

While a range of Amazonian species such as *Apistogramma* spp. and *Nannostomus* spp. were spotted around the vicinity of the traps (Supplementary Table 4.2), *Copella* and *Hemigrammus* dominated trap interactions. Despite the presence of non-target species, it is not believed that their presence impacted the focal species due to their low abundance and because they are typically found within the same habitat (Machado et al., 2020). Furthermore, only a small fraction of individuals that passed by or inspected traps ultimately entered them, a pattern consistent with findings from commercial food fisheries (Anders et al., 2017; Meintzer et al., 2017; Rose et al., 2005). The fact that only a small proportion of fish that passed by or inspected the trap actually entered suggests that there may be strong potential for selection for particular traits that influence trap entry, which differ between those that choose to enter the trap and the many that do not. Not only did a small proportion of fish enter the trap, but this was also not correlated with the number of inspections. For example, one trial saw 600 inspections compared to the usual mean of 80, yet no increase in the number of entries. The discrepancy between entries and inspections suggests that other factors - beyond the number of fish around a trap - ultimately influence the number of fish that enter and are captured.

Contrary to findings from other studies, such as Anders et al. (2017), which saw a difference in trap vulnerability between gadoid species in Northern Norway, I did not find a difference in overall capture rates between the two species. However, within a trial, traps tended to catch one species disproportionately. Therefore, while traps have the capacity to attract multiple species there may be differences between the focal species in environmental preference, interspecific variation in attraction to conspecific cues, or local variation in abundance, which can contribute to a given species being captured. Furthermore, while predator presence may have influenced the focal species, I found no evidence of predatory fish in the videos or during field sampling.

Interestingly, environmental variables such as temperature and dissolved oxygen did not affect the number of fish captured or the frequency of pre-capture behaviours like passes or inspections. This contrasts with studies such as Clark and Ioannou (2025), which found a greater number of captured sticklebacks in warmer water. However, date of capture significantly predicted the number of passes in my study, which may indirectly reflect changes in local environment or the composition of the population on a particular day. While the underlying mechanism remains inconclusive, it highlights how daily variation can have important repercussions for fisheries.

I found no difference between species in inspection or entry latency. The lack of a difference here could indicate that both species may have similarities in traits that determine the timing of an approach or entry. However, while there was no difference between species, water temperature played a key role as individuals inspected faster at higher temperatures. This finding aligns with studies that have linked temperature and boldness (Bartolini et al., 2015; Biro et al., 2009) and may be a function of increased activity at higher temperatures (Bartolini et al., 2015; Tiddy et al., 2024), which can increase the likelihood of an individual to encounter a passive gear (Hollins et al., 2018; Thomsen et al., 2010).

Previous research on commercial traps reveals a trend in the rate of entries (reviewed by Thomsen et al., 2010), with entries increasing, then levelling off, before declining. However, my results indicate that in artisanal fisheries, the rate of inspection and entry fluctuates. A reason for this difference could be that compared to commercial food traps, the artisanal traps used in this study were left for shorter periods, although this is more typical of the trap durations used by ornamental fishers. Nevertheless, I did find that the rate of inspection increased at higher dissolved oxygen levels, suggesting that environmental factors, particularly for fisheries within the Amazon, is an important driver of behaviour.

Very few behaviours around traps were temporally clustered, with synchronisation observed only for passes and inspections. The lack of coordination in entries challenges the assumption that sociability increases vulnerability to capture (Hollins et al., 2018; Thambithurai et al., 2018). Both *Hemigrammus* and *Copella* are schooling species (Ashraf et al., 2016), but the observed individual-level responses suggest that sociability may play a lesser role in final entry decisions than previously thought and that decisions to enter are made as individuals. This individual behaviour opens the door for selection to act on other components of behaviour at the individual level without social constraints operating. Species-specific responses to temperature were particularly striking in the context of coordination. In *Hemigrammus*, the coefficient of dispersion (CD) of inspections increased with water temperature, indicating more coordinated behaviour, while the opposite was true for *Copella*. Conversely, *Copella* displayed greater coordination in exits (higher CD) at higher temperatures, while the opposite trend was found for *Hemigrammus*. These contrasting patterns may reflect species-specific differences in how temperature influences activity levels, social behaviour, or behavioural plasticity. For example, increased water temperature may enhance group-level responsiveness in *Hemigrammus*, leading to more coordination when inspecting a trap, whereas *Copella* may exhibit more individual or variable responses. While the mechanisms underlying these contrasting patterns remains unclear, the variation in behaviour of the two species suggests that environmental changes may selectively affect trap vulnerability and behaviour in species-specific ways.

Importantly, the findings in this chapter represent a snapshot of the complex environmental dynamics within the Amazon. This study was conducted in the dry season, when increases in water temperature and reductions in dissolved oxygen levels are part of expected seasonal variation (Junk and Soares, 2010). However, as seasonal extremes are becoming more pronounced due to anthropogenic pressures (Espinoza et al., 2024; Ottoni et al., 2023), it is important to understand how changes in environmental conditions can modulate relationships between species-specific behavioural responses and their vulnerability to capture.

## 4.6 CONCLUSIONS

This study aimed to understand how fish behave around artisanal traps in the wild, how environmental factors influence the capture process, and whether differences could be observed between two Amazonian species. I found that the behaviour of fish around traps in the wild is complex, with only a fraction of fish that pass by or inspect a trap actually entering. While I found no difference in the capture rate or latency to inspect or enter a trap between species, traps typically caught one species over the other, and I observed species-specific variation in the timing and coordination of behavioural events, which were further influenced by environmental factors. Indeed, while environmental factors had no impact on the number of individuals caught, the time taken for an individual to inspect a trap was shorter at higher temperatures, and the rate of inspection increased at higher oxygen saturation levels. Importantly, the relationship between environmental factors and the coordination of behaviours varied between species. While warmer temperatures led to more coordinated inspections, but less coordinated exits for *Hemigrammus*, the opposite was true for *Copella*. Overall, the findings demonstrate that using a low-cost method to observe behaviours in uncontrolled settings provides a valuable insight into how traps work, particularly in artisanal settings. The findings also provide a more comprehensive understanding of the behaviours involved in the capture process, including pre-capture behaviours, and how environmental factors can drive differences between species.

# Chapter 5

# Behavioural differences among ornamental fish captured by different gears and exposed to thermal stress

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## 5.1 ABSTRACT

The harvest of animals from the wild is both intensive and selective, especially in fisheries, where non-random harvest can shape phenotypic composition and evolutionary trajectories. Central to understanding fisheries selection is determining whether certain traits render individuals more vulnerable to capture, which can vary depending on the type of capture method used. While there is increasing evidence that commercial and recreational fisheries can select for behavioural traits, smaller-scale artisanal fisheries such as the ornamental fishing trade have been overlooked in this context. The role of environmental factors in modulating relationships between phenotype and capture has also received little attention despite the well-established impacts of environmental factors such as temperature on a wide range of behavioural processes. Here, I investigated whether spotted tetra (*Copella nattereri*) caught by different gear types and exposed to different temperature regimes differ in behavioural traits. Fish were caught using active (nets) and passive (traps) gears and behavioural traits were quantified using an open field and novel object test. During the assays, groups of fish were exposed to either ambient or elevated (+3 °C) temperatures. Trap-caught fish were more exploratory and showed greater group cohesion, while net-caught fish

were more active. There was no difference in risk-taking between fish caught with different gears, and there was limited evidence that exposure to an elevated temperature influenced any behavioural traits apart from cohesion, which showed a negative correlation with temperature. Notably, a large proportion of variation was captured at the group-level, suggesting that group dynamics may mask individual behavioural responses, which has important implications for the potential of fisheries selection in the ornamental fish trade.

## 5.2 INTRODUCTION

Harvesting targets individual fish non-randomly. Across both commercial and recreational fisheries, there is a growing body of evidence showing that individuals vary in their vulnerability to capture, that vulnerability to capture is associated with intrinsic behavioural traits, and that different gear types tend to capture different behavioural phenotypes (Diaz Pauli and Sih, 2017; Koeck et al., 2020; Monk et al., 2021) For example, fish that are bolder, more active, and exploratory are typically more susceptible to passive gears including static hook-and-line angling and baited traps, as fish are more likely to encounter or interact with such gears (Arlinghaus et al., 2017; Diaz Pauli et al., 2015; Koeck et al., 2019). Alternatively, social individuals that exhibit stronger group cohesion may be more conspicuous to fishers and therefore disproportionately captured by more active gears such as trawls and purse seines (Guerra et al., 2020; Hollins et al., 2018a). While trait-based selection has received attention in commercial and recreational fisheries, it is currently not known whether similar patterns can be found in smaller-scale artisanal fisheries, despite their potential to also select for similar behavioural traits.

Small-scale fisheries provide crucial economic support to millions across the globe (King, 2019; OATA, 2020, 2016). One often overlooked sector is the ornamental fishing industry, a multi-billion-dollar trade that exports millions of fish annually (Evers et al., 2019; King, 2019). The Amazon Basin, in particular, is a major source of tropical freshwater species for the pet trade, and in some regions, wild-caught capture contributes up to 80% of household incomes (Chao et al., 2001; Evers et al., 2019; Tribuzy-Neto et al., 2021; Zehev et al., 2015). A huge diversity of species are targeted in the Amazonian ornamental trade, including the spotted tetra, *Copella nattereri* (Chao, 2001; Ferreira and Yamamoto, 2017; Ladislau et al., 2020; Prang, 2007). Spotted tetra are among a large number of ornamental species that are caught using a range of active and passive fishing techniques (Prang, 2007). A typical example of an active gear is the *rapiché*, a modified net used after fish are visually detected by fishers, whereas the *cacurí*, a baited trap, represents a commonly used passive gear (Ladislau et al., 2020; Prang, 2007). Although selection pressures in larger-scale fisheries have been documented, it remains unknown whether active and passive gears used in the ornamental trade also target fish non-randomly. If trait-based differences in behaviour were present, this could have important implications for the phenotypic composition of wild populations over time.

Central to understanding how individual traits relate to vulnerability to capture is the role of environment. Among environmental factors, temperature changes are particularly important for ectotherms such as fish, as even small fluctuations in temperature can affect a wide range of traits associated with capture (Hollins et al., 2021, 2018a). These include metabolic rate (Claireaux and Lefrançois, 2007; Hollins et al., 2021; Pilakouta et al., 2020), locomotor performance (Kuruvilla et al., 2023; Mittún et al., 2025), and behavioural traits such as risk-taking and group cohesion (Angiulli et al., 2020; Bartolini et al., 2015; Biro et al., 2009; Colchen et al., 2017b; Forsatkar et al., 2016; Pilakouta et al., 2023). For example, increased metabolic demands at higher temperatures have been linked to higher levels of activity and risk-taking behaviours in a range of fish species (reviewed by Tiddy et al., 2024). However, these changes can also reduce social cohesion due to greater levels of aggression and competition as individuals prioritise obtaining limited resources (Pilakouta et al., 2023). Such behavioural shifts can elevate the likelihood of encountering a given fishing gear, thereby increasing their vulnerability to capture (Stehfest et al., 2015; Stoner et al., 2006; Thomsen et al., 2010).

The relationship between temperature and behaviour is especially relevant in ornamental fisheries, particularly within the Amazon. The ornamental fishing trade occurs in the dry season, when stream drying leads to acute changes in temperature (Galacatos et al., 2004). While the behavioural impacts of temperature on ornamental Amazonian species are relatively less well-known, existing evidence suggests that elevated temperature influences aggression (Ribeiro et al., 2023), social hierarchy (Kochhann et al., 2015), and group coordination (Pineda et al., 2025), all of which could affect capture vulnerability. Understanding how environmental stressors such as temperature interact with capture is therefore critical to predicting how harvesting can shape the phenotypic composition of wild populations overtime.

Experimental approaches are useful for uncovering how temperature influences fish behaviour. A common approach involves thermal acclimation, where captive-bred or wild-caught fish are held at a constant temperature over days or weeks (De Bonville et al., 2025). This longer acclimation allows for more rigorous control over environmental conditions, which can be used to untangle mechanistic links among temperature, physiology, and behaviour. However, this control can come at a cost to realism by obscuring preexisting natural trait variation that may be observed *in situ*. An alternative approach is acute thermal exposure, where fish are subjected to rapid, short-term changes in temperature without prolonged habituation. Using this approach can reveal immediate behavioural responses to thermal shifts, which is particularly useful in dynamic environments such as the Amazon, where temperatures can fluctuate daily or over small spatial scales (Val and De Almeida-Val, 1995). *In situ* approaches, or experiments using recently captured fish, can therefore provide a middle ground, revealing behavioural outcomes at the time of capture, while in a relatively controlled setting (Binning et al., 2025). This is particularly useful in ornamental fisheries, where fish are often harvested under thermally stressful conditions, and where behaviours at the time of capture may influence both their vulnerability and post-capture survival.

Here, I examine whether the spotted tetra, an ornamental species caught by active and passive artisanal gears, differ in key behavioural phenotypes: exploration, activity (speed), cohesion, and risk-taking. I also explore whether acute exposure to elevated temperature alters these behavioural traits. I predicted that: i) fish caught by traps would exhibit greater risk-taking and exploration; ii) fish caught by nets would display greater group cohesion, and iii) elevated temperature would increase activity and boldness but decrease cohesion, potentially intensifying selective effects related to capture vulnerability.

## 5.3 METHODS

### 5.3.1 Fish Collection

Fish were collected in the Puranga da Conquista Sustainable Development Reserve (SDR) in the Brazilian Amazon (2°45'21.4"S 60°25'04.3"W) during the dry season for five days in September 2022. Sampling was done each morning, using an active and passive gear. The passive gear was a *cacurí*, an artisanal static trap baited with rice and manioc powder (Figure 5.1A). The active gear was a *rapiché*, a modified net, commonly used by fishers in the ornamental fishing industry Figure 5.1B).

**Figure 5.1)** Artisanal traps used in ornamental fishing industry: A) *cacurí* - a cylindrical trap made of fine mesh (45 x 28 cm) with a narrow funnel-shaped opening (5 cm wide); B) *rapiché*- a modified hand net (50 x 40 cm). Photos by M Pineda and S. S. Killen.

Traps were placed by experimenters so that the top of the trap emerged from the surface of the water, as is typical within the ornamental fishing industry (Prang, 2007) and were left undisturbed for 30 minutes. Meanwhile, fish were netted using the *rapiché* within the same field site but downstream from the traps (~30-50 m away). Only the target species, the spotted tetra (*Copella nattereri)*, was retained, and all other species were released to their original collection site. Environmental variables: air temperature, water temperature, pH, and dissolved oxygen, were also measured at each sampling site (Supplementary Table 5.1) using a YSI meter (YSI Pro20). After fish collection each morning, spotted tetra were transported to a nearby temporary lab at the SDR. Fish were transported in insulated containers (80 L x 40 W x 40 H cm) by boat, with transport lasting ~30 minutes. In the lab, fish were acclimated for 3-5 hours at ambient water temperatures. Experiments were then carried out the same afternoon.

### 5.3.2 Open Field and Novel Object Tests

Fish were tested in groups of six, a commonly used number in behavioural studies, given that it is a large enough number that social dynamics can be observed in a group, while being manageable for video analysis and reliable tracking of individuals (Anderson et al., 2020; Hockley et al., 2014; Latchem et al., 2025; Lonhus et al., 2023). Groups were randomly placed into one of four treatment groups according to collection method and testing temperature: 1) *Rapiché*-Control; 2) *Rapiché*- Warm; 3) *Cacurí*-Control, and 4) *Cacurí*-Warm. Environmental conditions in the temporary lab were intended to reflect natural environmental fluctuations in the wild, and therefore acclimation temperature was not maintained at a constant temperature throughout the experiment. Instead, the control temperature was based on the mean water temperature during collection on the day (ambient), and the warm treatment was the control temperature + 3 °C. The warm treatment was chosen to reflect the increase of 3°C predicted by climate change models for tropical water surface temperatures (Campos et al., 2019). Water temperature was regulated by adding warmed water to the arena until the desired acclimation temperature was reached. Throughout the study, temperatures were obtained with a YSI meter (YSI Pro20) which has an accuracy of ± 0.2 °C. Ambient, control, and warm temperatures throughout the experiment are demonstrated in Figure 5.2.

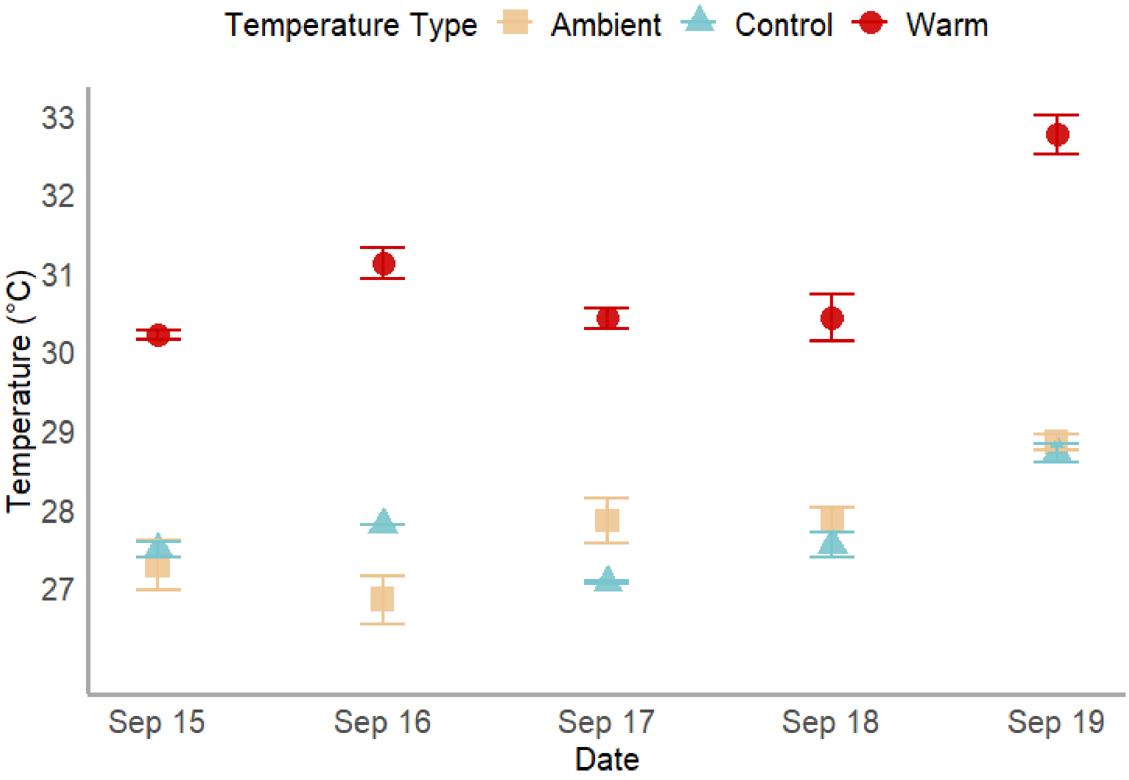

**Figure 5.2)** Mean (± SE) temperatures across the five sampling dates under three temperatures: Ambient, Control, and Warm. Data points represent treatment means and error bars indicate standard error of the mean. The number of trials differed across temperature types and dates. Ambient temperatures were collected during fish collection and were more numerous (n = 9-17 per day). Control and warm temperatures were collected before the start of each trial (n = 3-5 per day for control and n = 2-4 per day for warm).

Open field and novel object tests were conducted in a rectangular arena (60 x 40 cm) filled with water to a depth of 6 cm. For the open field test, groups were introduced into the behavioural arena and allowed to acclimate freely for 5 minutes. After the acclimation period, fish were allowed to explore the arena freely for a further 5 minutes. Immediately after the open field test, a novel object (small submersible yellow toy: 5 x 7 cm) was introduced into the behavioural arena. The novel object was placed in a fixed location across trials to ensure consistency. Fish were then allowed to explore the arena freely for an additional 5 minutes. After each trial, the water was fully replaced to eliminate chemical social cues, and all individuals were measured for standard length (SL) and total length (TL). A total of 20 open field and 20 novel object trials were conducted (n = 10 groups per capture method), and all trials were recorded using a video camera (GoPro Hero 4) mounted above the arena.

The experimental procedures were approved by the Animal Use Ethics Committee of the Brazilian National Institute for Research of the Amazon (CEUA-INPA), number 01280.000209/2018-74. The permit for the collection of the biological material to carry out the research was authorized by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA/SISBIO), number 29837-13.

### 5.3.3 Video Analysis

Videos were analysed using Ethovision XT 15 (Noldus Information Technology, Wageningen, The Netherlands). For open field trials, analysis began immediately after the end of the acclimation period. Data were extracted for each individual for 5 minutes. For the novel object test, video analysis began after the novel object was placed into the arena. The novel object videos were also analysed for a total of 5 minutes. The movement of individuals during the trial was tracked and extracted to quantify the behavioural metrics listed in Table 5.1.

**Table 5.1)** Summary of behavioural metrics extracted from video analysis.

| **Behaviour** | **Description** |
|---|---|
| Risk-taking $_{\text{Arena}}$ | Mean distance (cm) from a fish to the centre of the arena. |
| Risk-taking $_{\text{Novel Object}}$ | Mean distance (cm) from a fish to the novel object. |
| Exploration | Total distance (cm) moved by an individual. |
| Activity | Average moving speed (cm $s^{-1}$) of an individual, calculated as total distance moved divided by time spent moving. |

| | |
|---|---|
| Cohesion | Average neighbour distance (AND), defined as the mean distance (cm) between an individual and all other group members. |

### 5.3.4 Statistical Analyses

All statistical analyses were carried out in R (version 4.4.1). To explore the behavioural traits of fish caught by different gears and exposed to different temperature treatments, a series of linear mixed effects models were fitted using the lme4 package (Bates et al., 2015). For the open field test, activity, average neighbour distance, and risk-taking $_{A}$ were used as response variables. Temperature (control or warm), gear type (net or trap), group average total length, and group variation in total length were used as explanatory variables. An interaction between gear type and temperature was also included to test whether fish caught by different gear types exhibit different behavioural responses depending on testing temperature. Group was also included as a random factor to account for variation caused by group effects. The same model structure was used to analyse the novel object tests with the additional fixed effect of risk-taking $_{NO}$. For all models, model simplification was performed in a stepwise manner using likelihood ratio tests to identify the most parsimonious model for each response variable.

## 5.4 RESULTS

Differences in cohesion were revealed between individuals caught with different gear types (Figure 5.3). Net-caught fish had greater average neighbour distances and were less cohesive in both open field (Estimate = 6.00 ± 1.05 SE, t = 5.69, p = <0.001) and novel object tests (Estimate = 3.01 ± 0.95 SE, t = 3.17, p = 0.003). Additionally, while there was no influence of temperature on cohesion in the open field test (Supplementary Table 5.2), in the novel object test, groups in the warm treatment were less cohesive than in the control groups (Estimate = 1.98 ± 0.95 SE, t = 2.08, p = 0.044). Furthermore, while gear type and temperature treatment explained variation in cohesion in the novel object test, there was no evidence of an interaction between the two (Supplementary Table 5.3).

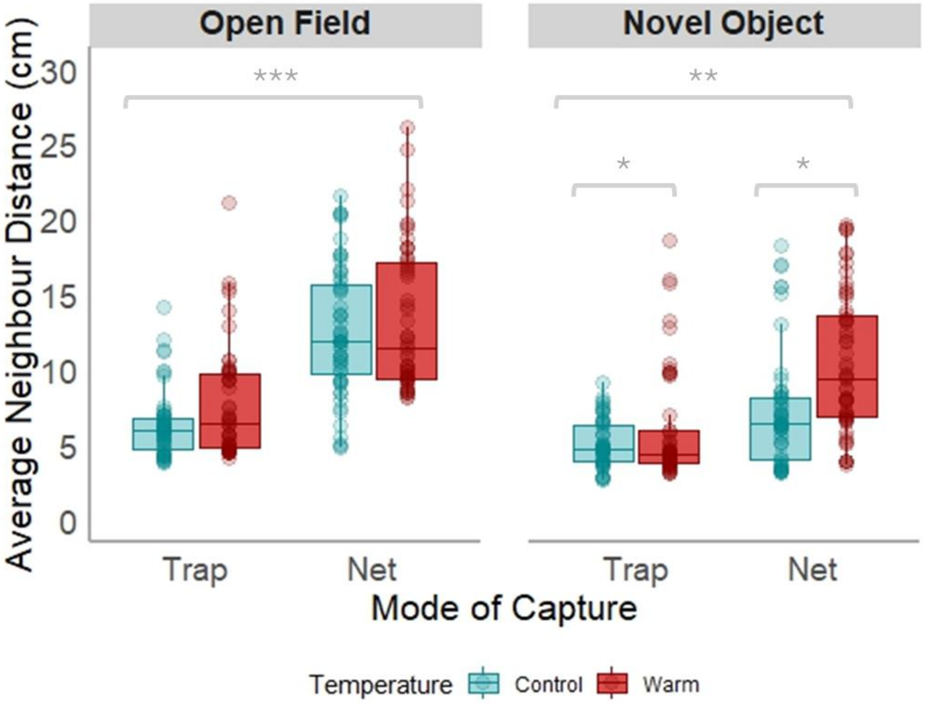

**Figure 5.3)** Differences in cohesion between fish caught by different gears and exposed to an elevated temperature during open field and novel object tests. Each data point represents an individual. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****).

Fish caught by different gears also exhibited differences in exploration (Figure 5.4). Trap caught fish were more exploratory in both the open field (Estimate = -210 ± 49.62 SE, t = -4.24, p = <0.001) and novel object tests (Estimate = -211.10 ± 68.77 SE, t = -3.07, p = 0.004). There was no evidence that temperature affected exploratory behaviour or interacted with gear type in either assay (Supplementary Tables 5.2-5.3). However, groups differed in exploratory behaviour, particularly in the novel object test as the random effect explained over 60% of the variation (Supplementary Table 5.3).

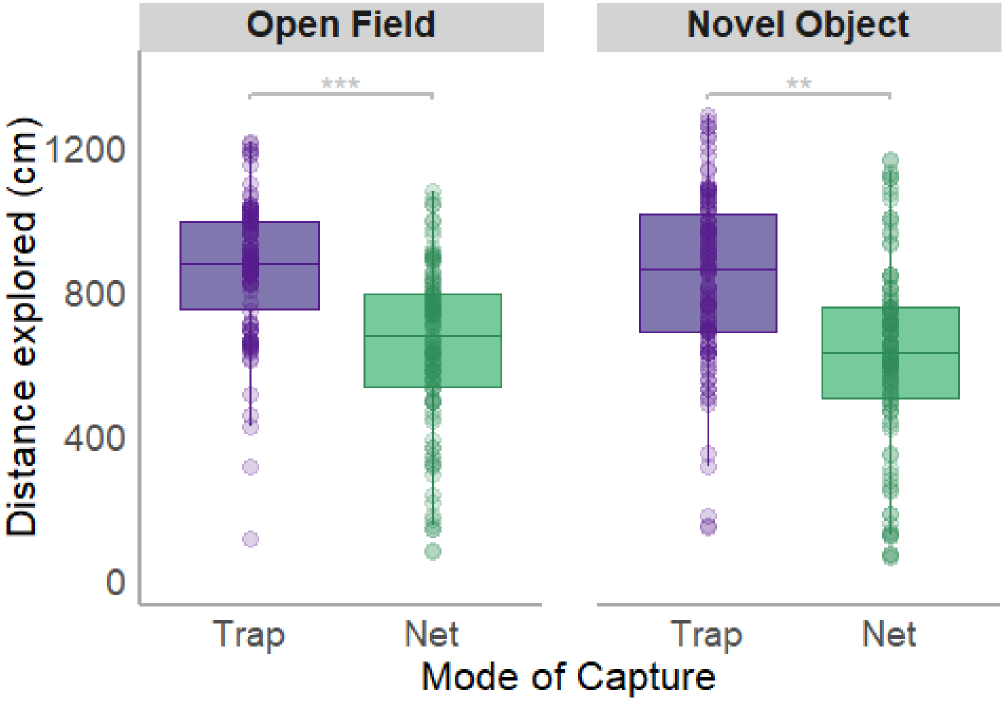

**Figure 5.4)** Differences in exploration between fish caught by different during open field and novel object tests. Each data point represents an individual. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****).

Fish caught by different gears also differed in activity levels (Figure 5.5). Net caught fish had greater moving speeds in open field (Estimate = 1.26 ± 0.64 SE, $t = 1.99$, $p = 0.048$) and novel object tests (Estimate = 1.51 ± 0.64 SE, $t = 2.34$, $p = 0.020$). However, there was no evidence that temperature influenced activity in either assay (Supplementary Tables 5.2-5.3).

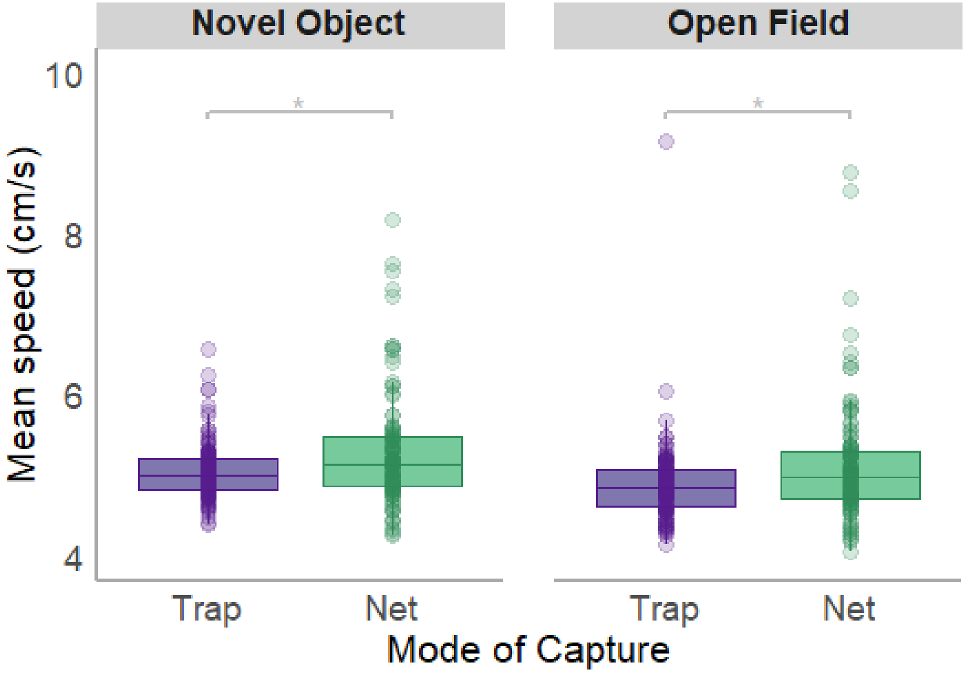

**Figure 5.5)** Differences in activity (speed) between fish caught by different gears during open field and novel object tests. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****).

There was no difference in risk-taking measured as distance to the centre of the arena, or distance to a novel object, between fish caught by different gears (Supplementary Tables 5.2-5.3). Additionally, while there was a marginal non-significant difference in risk-taking in the warm treatment (Supplementary Figure 5.1; Supplementary Table 5.3), there was no overall evidence that temperature influenced risk-taking (Supplementary Tables 5.2-5.3). However, there was a large amount of variation in risk-taking between groups, ranging from 53-81% (Supplementary Tables 5.2-5.3).

## 5.5 DISCUSSION

Identifying which traits differ between individuals caught by different gear types is crucial to understanding how non-random harvest can drive selection in exploited populations. While behavioural traits such as activity, exploration, boldness, and group cohesion are linked to capture vulnerability (Álvarez-Quintero et al., 2021; Diaz Pauli et al., 2015; Hollins et al., 2018a), they can also be influenced by environmental factors including temperature (Hollins et al., 2021). Here, using natural populations of spotted tetra, I tested whether fish caught by active (nets) and passive (traps) gears differed in behavioural traits and if behavioural traits were affected by exposure to an elevated temperature. The results show that fish caught by different gears exhibit consistent differences in behavioural traits, with little evidence that increased temperature affected most behavioural traits. The findings also highlight that there is substantial variation among social groups, which may influence behavioural outcomes, displaying the complexity of pin-pointing the basis for trait-based selection in this fishery.

Fish caught using traps showed greater group cohesion compared to those caught with nets, even in the presence of a novel object. This mirrors findings by Álvarez-Quintero et al (2021), who found that in three-spined stickleback, (*Gasterosteus aculeatus*), trap-caught fish spent a greater proportion of time with conspecifics. The spotted tetra is a naturally gregarious species in the wild, so individuals may be more likely to follow others into a trap (Thambithurai et al., 2018). However, recent observations of traps in the Amazon have suggested that spotted tetra do not enter traps in groups (Pineda et al., 2025). Further studies are therefore needed to determine links between social behaviours such as cohesion, and capture. In this study, cohesion was also affected by temperature, with increased temperature decreasing cohesion, aligning with studies showing that cohesion can decrease under thermal stress by increasing metabolic demands and reducing group coordination (Pilakouta et al., 2023). Interestingly, temperature effects were only apparent in the novel object test, suggesting that responses to temperature may be more apparent with a combined stressor of a novel object.

Trap-caught fish were more exploratory but also less active, moving at slower speeds compared to net-caught fish. While exploratory behaviour has previously been linked to capture by passive gears in other studies (Arlinghaus et al., 2017; Monk et al., 2021), the decoupling between exploration and activity is surprising, as these traits are often positively correlated (Angiulli et al., 2020). One possible explanation is that exploratory behaviour in the spotted tetra may not be linked to speed of movement, especially within a confined experimental arena (Kuntz et al., 2024). Additionally, no effect of temperature was observed on either exploration or activity, contrasting with findings showing that higher temperatures often lead to increased movement and risk-taking (Biro et al., 2009; Forsatkar et al., 2016). A possible reason for the lack of finding in this chapter, is that wild-caught fish in the Amazon are regularly exposed to diurnal and seasonal temperature variations (Val and De Almeida-Val, 1995), so may be more resilient to acute changes compared to lab-acclimated individuals. It is therefore important to consider whether previous lab-based findings between temperature and behaviour are generalisable to field conditions where thermal variability is the norm.

Notably, there was no difference in risk-taking behaviour between fish caught by different gears. This was in direct contradiction to my hypothesis and with previous findings that have often shown that fish caught by passive gears exhibit risk-taking behaviours (Arlinghaus et al., 2017; Diaz Pauli et al., 2015; Monk et al., 2021). I also found no relationship between risk-taking behaviour (measured as the distance from the wall, or distance to the novel object) and temperature despite previous studies linking temperature and boldness (Biro et al., 2009; Forsatkar et al., 2016). The relationship between temperature and risk-taking is often driven by differences in activity or foraging drive, which enhances exploratory behaviour (Pilakouta et al., 2023). In this study, neither of these traits were affected by temperature, suggesting a consistent behavioural pattern across traits. This is particularly important as water temperatures in the Amazon have increased dramatically recently, far beyond the temperatures used in this study (Espinoza et al., 2024; Ottoni et al., 2023). Further research should explore the impacts of behavioural traits at these new temperatures experienced by Amazonian fish species.

Importantly, I also found a considerable amount of behavioural variation among groups, which masked individual responses in this study. Group level effects have been increasingly recognised in behavioural ecology, particularly within the context of collective behaviour, where individuals compromise their own traits to maintain group cohesion (Jolles et al., 2020; Killen et al., 2018; Pineda et al., 2020). This group level variation also highlights the difficulty in predicting capture vulnerability, as selection may operate depending on the particular phenotypic composition of a group at the point of capture. In ornamental fisheries, where entire groups can be captured at once (Ladislau et al., 2020; Prang, 2007), understanding how group composition affects vulnerability to capture is vital.

## 5.6 CONCLUSIONS

My study aimed to understand whether the behavioural traits of an ornamental species differed between captured methods, and if behavioural traits were influenced by an increase in temperature. I found consistent differences in behavioural traits between fish caught by passive (traps) and active (nets) methods. Trap-caught fish were more exploratory, and cohesive, whereas net-caught fish were more active. I found no difference in risk-taking between fish caught by different captured methods, and I found limited evidence that elevated temperature influenced behavioural traits beyond cohesion. Notably, there was also a considerable amount of behavioural variation among groups, which masked individual behavioural responses. Taken together, my findings have important implications for understanding how selection may operate in a small-scale artisanal fishery. Although ornamental fisheries are less intensive than commercial fisheries, I show that they may still non-randomly target behavioural phenotypes, especially if a given gear is consistently used to capture fish. The findings also highlight that a failure to account for group effects may lead to under or over estimation of trait variation in natural populations. Future research should examine differences in traits between individuals and groups, to understand the role of collective behaviour in shaping vulnerability to capture.

# Chapter 6

# General Discussion

Understanding the extent to which human activities act as a selective force has been a major focus of ecological and evolutionary research (Baltazar-Soares et al., 2021; Hendry et al., 2017; Palkovacs et al., 2012). Among the myriad forms of human-induced selection, harvesting is consistently cited as one of the most intensive and selective (Allendorf et al., 2008; Allendorf and Hard, 2009; Darimont et al., 2015, 2009; Kuparinen and Festa-Bianchet, 2017). Commercial and recreational fisheries have demonstrated that non-random removal of individuals with certain traits can alter the phenotypic composition of wild populations (Hollins et al., 2018b), and in exploited stocks, can lead to fisheries-induced evolution (FIE) (Enberg et al., 2009; Heino et al., 2015, 2013; Monk et al., 2021). While most studies to date have focused on life-history traits such as age at maturation (Enberg et al., 2012; Ernande et al., 2004; Uusi-Heikkilä et al., 2015), there has been a more recent shift towards understanding how behavioural and physiological traits may also be under selection (Andersen et al., 2018; Arlinghaus et al., 2017; Bieber et al., 2023; Diaz Pauli and Sih, 2017; Hollins et al., 2018b).

Despite growing interest in the behavioural and physiological mechanisms underpinning capture vulnerability and consequent selection, several gaps remain in our understanding. For example, almost all existing work has focused on large-bodied species in commercial or recreational fisheries (Arlinghaus et al., 2017; Cooke et al., 2007; Koeck et al., 2020; Stehfest et al., 2015), with small-scale and artisanal fisheries completely overlooked. Additionally, although studies have found that behavioural and physiological traits influence capture outcomes in the lab (Crespel et al., 2021a; Diaz Pauli et al., 2015; Hollins et al., 2019; Killen et al., 2015; Thambithurai et al., 2022) and in the field (Cooke et al., 2007; Klefoth et al., 2017; Koeck et al., 2020), very few have considered how environmental context such as temperature or oxygen availability can modulate these relationships (but see Hollins et al., 2021 and Thambithurai et al., 2019). This is surprising given the established effects of environmental variables on trait expression (Biro et al., 2009; Killen et al., 2013; Pilakouta et al., 2023, 2020; Tiddy et al., 2024) and even trait heritability (Charo-Karisa et al., 2005; Doyle et al., 2011). Moreover, while passive and active gear types have been shown to capture fish with particular phenotypes (Álvarez-Quintero et al., 2021; Diaz Pauli et al., 2015; Hollins et al., 2018a; Sun et al., 2022), the extent to which this occurs in artisanal fisheries had not been investigated.

Finally, while most research has focussed on the outcome of capture, very few explore the behavioural processes preceding capture (Thomsen et al., 2010), and how this can vary across species or environmental contexts.

In this thesis, I addressed these knowledge gaps using a combination of lab-based simulations and experiments, and field-based observations across multiple ornamental species and environmental contexts. I investigated whether morphological, behavioural, and physiological phenotypes were linked to vulnerability to capture, whether different artisanal gears captured individuals with different traits, and if environmental conditions influenced relationships between phenotype and gear type. Here, I summarise key findings from each chapter, overarching themes across chapters, and then discuss the implications for selection in the ornamental trade as well as highlighting key challenges and future directions.

## 6.1 Summary of Key Findings

In chapter 2, I used a scaled-down trapping simulation in a controlled lab environment using wild-caught cardinal tetra. The main objective of this chapter was to identify individual variation in capture vulnerability and to ascertain if this could be predicted by morphological, physiological, and behavioural traits. Repeated capture trials revealed that individuals varied in capture vulnerability, with some fish never entering traps (low vulnerability), some fish always entering traps (high vulnerability), and some fish showing mixed responses. Probability of capture was higher in fish that were bolder (measured as a shorter latency to emerge from acclimation zone), more exploratory, and more active. Probability of capture was also higher for fish that were smaller and that fatigued faster, suggesting lower endurance or anaerobic capacity. These findings provided the first evidence that ornamental species display trait-based vulnerability to capture.

Chapter 3 extended the lab-based findings on traps by comparing wild-caught tetra captured in the Rio Negro using a passive gear (trap) as well as an active gear (net). After capture, cardinal tetra were transferred and acclimated to lab setting and tested for a suite of behavioural and physiological traits. Net-caught fish were smaller but had a greater swimming performance (measured as maximum swimming speed) when corrected for body mass. Behavioural traits were quantified using a range of behavioural assays including a maze test, an open field test, and a novel object test, which were designed to test behaviours under different levels of complexity. Some behaviours were linked to a specific gear type consistently. Trap-caught fish were more exploratory, but net-caught fish were faster, and therefore more active. Net-caught fish were also more cohesive in the maze test and the open field and novel object tests, with net-caught fish spending more time together and have shorter average neighbour distances. Surprisingly, differences in risk-taking were minimal across most assays, with the exception of the maze test, where the most risk-prone individuals were trap-caught. Interestingly, in this chapter, even small fluctuations in temperature (0.4°C) influenced behavioural traits such as activity, exploration, and cohesion, highlighting the need to consider environmental context.

While chapters 1-3 tested and compared traits of captured individuals, chapter 4 examined the behaviour of fish around traps in the wild. This provided novel insights into the capture process, including pre-capture behaviours, such as passes and inspections, which are rarely explored in the context of fishing selection (Pineda et al., 2025). Underwater video recordings were used to observe the natural behaviour of two ornamental species, the spotted tetra (*Copella nattereri*) and *Hemigrammus* spp. The majority of fish that approached a trap did not enter it, and among those that did, entry was typically uncoordinated, although individuals entered a trap faster if there were more individuals inside the trap. Latency to approach the trap was influenced by environmental temperature, with higher temperatures associated with quicker responses. Additionally, while the likelihood of capture was similar between species, once a given trap caught one species, the likelihood of capture for the other was lower. There were also differences between species in how environment modulated behavioural responses, but patterns varied across behaviours. Overall, the findings from this chapter indicated that trap entry is not random and that interactions between species and environmental conditions must be considered.

In chapter 5, I revisited differences in behavioural traits between fish captured using different gear types, but this time using the spotted tetra and focusing on behaviours under ambient and elevated temperatures. Fish were tested in open field and novel object tests shortly after capture using traps or nets and some fish were exposed to an acute increase in temperature. Net-caught fish were faster than trap-caught fish, mirroring findings in chapter 3. However, net-caught fish were less cohesive, which contradicted findings in chapter 3. The difference in results between these two chapters suggests that the effect of capture method on group cohesion may be context dependent. For example, differences in acclimation time between the two studies may have influenced post-capture recovery as fish in chapter 3 were given longer to acclimate. Alternatively, the contrasting patterns may reflect species-specific differences in shoaling or stress response. Surprisingly, acute temperature increase had limited effects on behaviour, with the exception of group cohesion, where a relationship was only revealed after exposure to a novel object. However, variations in individual behaviour were largely masked at the group level, with the random factor of group identity accounting for a large proportion of the explained variation. This chapter therefore highlighted that group composition can play an important role in shaping collective behaviours and in the potential for selection.

## 6.2 Overarching Themes

### 6.2.1 Predicting Vulnerability to Capture

A core aim of this thesis was to determine if individual phenotypes influence vulnerability to capture in the ornamental fishing trade. Chapter 2 provided clear evidence that capture vulnerability in the cardinal tetra is influenced by morphological, physiological, and behavioural traits. Specifically, bolder, more active, and exploratory individuals were more likely to be trapped, findings that are consistent with patterns observed in commercial and recreational fisheries (Diaz Pauli et al., 2015; Hollins et al., 2018a; Koeck et al., 2019; Monk et al., 2021). These results also lend further support for the "timidity syndrome" proposed by Arlinghaus et al. (2017), in which repeated removal of bold individuals leads to a reduction in risk-taking behaviours in the remaining population. Body size was also a strong predictor of vulnerability to capture as smaller individuals were captured more frequently. This mirrors observations in commercial fisheries, where size-selective harvesting is a crucial driver of phenotypic and evolutionary change (Enberg et al., 2012; Heino et al., 2013; Uusi-Heikkilä et al., 2015). This trait-based vulnerability supports the idea that ornamental fishing, like other forms of harvesting, can act as a selective force. While previous studies have often relied on surrogate species (Crespel et al., 2021b; Killen et al., 2015; Thambithurai et al., 2018) this study used the actual target species in a gear-relevant simulation, strengthening the ecological relevance of the findings. As ornamental capture also appears to be linked to analogous behavioural and morphological traits, it suggests that similar selective pressures may exist in these smaller, non-consumptive fisheries.

However, an important aspect to acknowledge is that predictions of vulnerability to capture are largely context-dependent (Hollins et al., 2018). As chapter 2 was conducted under controlled laboratory conditions, environmental variables such as temperature and oxygen were highly controlled, and fluctuations were minimal. In reality, it is well-established that behavioural and physiological traits are highly plastic and are modulated by environmental factors (Abdelnour et al., 2024; Hollins et al., 2021), as such, any changes in environmental factors may have resulted in different behavioural or physiological responses. Therefore, while the findings from chapter 2 were informative, predictions of capture vulnerability must integrate environmental context.

### 6.2.2 Comparing Traits Between Gear Types

While chapter 2 was focussed on predicting capture vulnerability, chapters 3 and 5 observed differences in pre-existing phenotypes between individuals caught by active and passive gear types. The chapters explored two ornamental species, the cardinal tetra, and the spotted tetra, both of which are targets of the Amazonian ornamental trade that are captured using both gear types (Ladislau et al., 2020). In both species, trap-caught fish were generally more exploratory, mirroring findings from commercial and recreational fisheries (Diaz Pauli and Sih, 2017). In contrast, net-caught fish were more active, and showed higher group cohesion, contrasting with previous work on three-spine stickleback which suggested that trap-caught fish were more cohesive (Álvarez-Quintero et al., 2021). Nevertheless, differences in our findings were observed across environmental and experimental contexts, suggesting a consistency and repeatability of patterns within these ornamental species.

Interestingly, differences in risk-taking between gear types were minimal, despite risk-taking behaviours typically being associated with capture from passive gears in commercial and recreational fisheries (Andersen et al., 2018; Arlinghaus et al., 2017; Monk et al., 2021), and risk-taking being a key predictor of individual vulnerability to capture in chapter 2. In Chapter 3, gear differences in risk-taking only emerged when analysing the boldest individuals within groups, with trap-caught fish displaying shorter emergence latencies. In contrast, no group-level differences were found. Similarly, in Chapter 5, individual-level differences in risk-taking were initially detected but disappeared after accounting for group identity. These findings provide a crucial insight; that behavioural outcomes differ at individual and group levels (Jolles et al., 2020; Pineda et al., 2020). All species studied in this thesis are considered to be social, and traits such as risk-taking, exploration, and activity can be modulated by group composition (Jolles et al., 2020). While selection operates on the individual level, the expression of traits under selection occurs within the group, meaning that collective behaviours may amplify or mask individual-level vulnerabilities to capture.

### 6.2.3 Exploring Environmental Context

A recurring theme across chapters 3 to 5, is the role of environmental factors in shaping how behavioural traits are expressed, which in turn, has important repercussions for vulnerability to capture (Hollins et al., 2021, 2018). While rarely expressly tested in fisheries selection research (but see Hollins et al., 2021), temperature variation, both natural and experimental, consistently influenced fish behaviour in this thesis. In chapter 3, ambient temperatures were not manipulated, but the small variations in ambient temperature that did exist, were statistically integrated. This is notable, as although temperature can affect a suite of behavioural and physiological traits (Angiulli et al., 2020; Bartolini et al., 2015; Tiddy et al., 2024), ambient temperature is rarely reported or statistically accounted for during experiments. Indeed, I found that even small increases in temperature reduced cohesion, increased activity (speed), and exploration, mirroring existing findings (Angiulli et al., 2020; Biro et al., 2009). In chapter 4, environmental variables, namely temperature and oxygen availability, were recorded *in situ.* Here, temperatures increased risk-taking behaviours such as latency to approach and inspect a trap and also influenced the coordination of behaviours, although the pattern differed between the studied species (spotted tetra and *Hemigrammus*). These findings suggest that environmental variation influences pre-capture behaviours that may be under selection. These observations also build on previous work showing that temperature can modulate risk-taking behaviours (Biro et al., 2009) and demonstrate that such modulation can occur even under field conditions, although differences and interactions between species must still be accounted for. Chapter 5 introduced a direct manipulation of temperature, where groups were subjected to an acute increase in temperature shortly after capture. Although behavioural differences between temperature treatments were more limited than expected, cohesion was also reduced in the elevated temperature treatment, mirror findings from chapter 3. Importantly, this chapter also revealed that group composition accounted for a large proportion of variation in behavioural expression, suggesting that temperature effects may interact with social context.

Overall, these findings highlight the importance of considering and integrating environmental context. Understanding how environmental factors influence the behaviours of individuals and groups is not only important for understanding how fish may respond to environmental changes, but also for predicting vulnerability to capture and understanding repercussions for fisheries selection. This is especially important as many of the traits which may be under selection are not necessarily fixed, but are phenotypically plastic (Abdelnour et al., 2024), therefore selection pressures imposed by fishing gears may vary across thermal regimes. Environmental changes are particularly relevant in the Amazon, where climate change is expected to increase temperature variability and extreme events such as droughts (Ottoni et al., 2023). If relationships between environment and phenotype shift due to climate change, then so too will relationships with vulnerability to capture.

## 6.3 Implications for Fishing-Induced Selection

Together, the findings in this thesis suggest that even small-scale, artisanal fisheries have the potential to exert selective pressures on wild populations. Below, Table 6.1 summarises what was known in the field of fishing-induced selection, what the missing gaps were in our knowledge, and what my findings add to the existing body of work. It also highlights the implications for fishing-induced selection in the ornamental fishing industry.

**Table 6.1)** Summary of how thesis findings and implications contribute to existing knowledge.

| Chapter | Existing Knowledge | Knowledge Gaps | Novel Insights | Implications for Fishing-Induced Selection | Implications for Ornamental Fishing Industry |
|---|---|---|---|---|---|
| 2 | Behavioural and physiological traits can be linked to capture vulnerability in scaled-down simulations of commercial fisheries. | Unknown whether this could occur in smaller scale artisanal fisheries like the ornamental fishing industry. | Morphological, behavioural, and physiological traits predict capture vulnerability in an ornamental species. | Trait-based vulnerability confirms potential for directional selection in ornamental fisheries. | Ornamental capture is also non-random for traits unrelated to aesthetics. Suggests long-term selection could be possible. |
| 3 | Fish caught with active and passive gears in commercial and recreational fisheries have distinct phenotypes. | Not clear which traits are captured, and findings are inconsistent and context dependent. Not examined in ornamental fisheries. | Ornamental fish caught with different gears have distinct phenotypes, which can be further influenced by environmental factors. | Active and passive gears could impose divergent selection pressures. Environmental context is important for predicting selective impacts. | Highlights the potential impacts of using one particular artisanal gear consistently. |
| 4 | Some studies have shown behaviours can vary around commercial pots, and some environmental variables can influence behaviour. | Fisheries selection has not focussed on pre-capture behaviours. Never investigated in ornamental fisheries. | Field-based evidence that temperature influences pre-capture behaviour, and species differ in how environment modulates behaviour. | Environmental context can change selection dynamics, potentially shifting which individuals are captured. | Suggests climate-driven changes in the Amazon, such as droughts, may alter which fish get captured, affecting trait distributions over time. |
| 5 | Environmental factors influence behavioural and physiological traits that are related to capture vulnerability. | Few studies directly test capture vulnerability and temperature. Never in ornamental fisheries. | Ambient temperatures influence behaviours. Differences in behaviour at the individual and group-level. | Group context could mask or amplify selection on individual traits. | Within social ornamental species, it can be difficult to select outcomes of fishing selection. |

## 6.4 Limitations and Future Directions

The findings from this thesis provide a foundation for understanding the potential selective effects of fishing in the ornamental trade, nevertheless, there are some limitations that must be addressed. Here, these are categorised under methodological constraints, challenges with quantifying selection, and gaps in our evolutionary understanding of ornamental species. Finally, future directions of research are outlined to provide next steps in this field.

### 6.4.1 Methodological Constraints

One of the limitations of this thesis lies in the experimental approach used in my first data chapter. Chapter 2 used a lab-based simulated approach using wild-caught cardinal tetra imported from a specialist supplier. While cardinal tetra are often imported from the wild due to difficulties with breeding in captivity (Evers et al., 2019), it was not possible to source the exact location the cardinal tetras came from, or what gears had been used to capture them. Although my approach allowed for a controlled lab setting to uncover important mechanisms between phenotype and capture vulnerability, it is possible that prior environmental conditions may have shaped observed behavioural and physiological traits. As I tested a subset of the population that had already been captured, it is also possible that selection may also have been stronger in this subset. Additionally, the trapping scenario forced fish into closer proximity to the gear, increasing the probability of approaching and entering a trap, and forcing fish into a binary decision to enter or not. While this is a common constraint of a method that has been used by others previously (Hollins et al., 2021; Thambithurai et al., 2022, 2018), it may not reflect the realistic capture process that I demonstrated in chapter 4.

### 6.4.2 Understanding Selection

Across many chapters of this thesis, one of the main logistical challenges was not being able to test phenotypes of fish that had not been captured. While chapter 4 did provide some insights into pre-capture behaviours such as passes and inspections, as well as post-capture behaviours such as escapes, I was not able to compare traits between captured and non-captured individuals. Another important aspect which would greatly improve our understanding of selection is knowledge of natural vs fishing mortality in ornamental fisheries. Although ornamental species are typically caught in the dry season, where there is natural mortality, it is not known how natural mortality compares to the volume of fishing within the ornamental trade, which has been notoriously difficult to ascertain (King, 2019). Therefore, despite being able to make inferences in differences between gear types and environmental modulations of behaviour, it remains difficult to estimate how frequently phenotypes are removed from a population, unless there is an increase in population-level monitoring.

### 6.4.3 Evolutionary Uncertainties

Another constraint in this thesis is the lack of information on the heritability of traits related to capture vulnerability in ornamental species. While many of the measured traits such as swimming performance and exploration have been shown to be heritable in other taxa (Ariyomo et al., 2013; Kortet et al., 2014), this has not yet been quantified in Amazonian ornamental species. Understanding the heritability of these traits would be a key step toward answering evolutionary questions. Another challenge involved with determining the potential for evolution is the lack of genomic resources in many ornamental species, which limits the application of modern genomic approaches. Overall, this has made it challenging to understand how selection may act on genotypes, and not just phenotypes, or to untangle contributions of phenotypic plasticity and true evolution. Nevertheless, an important step towards understanding the potential for evolution is uncovering trait variation and selective pressure, which I have now provided a foundation for in this thesis.

### 6.4.4 Future Directions

Moving forward, there are several next steps that could build on the findings of this thesis. As mentioned in the above section, determining trait heritability of behavioural and physiological traits related to capture is key for understanding long-term impacts of fishing. Establishing longitudinal breeding experiments in ornamental species would be a critical step towards understanding whether observed differences are able to result in real evolutionary change. Combining this with novel methods in quantitative genetics would also be very useful for linking capture vulnerability to selection (as in Crespel et al., 2021).

Characterising traits of individuals that have not been captured will further enhance our understanding of fisheries selection generally, but also in the context of ornamental fisheries. While this may be challenging to achieve using lab-based experimental approaches, continued underwater observations in an enclosed area or mesocosm may also provide a realistic alternative. Further insight could also be gained by comparing populations exposed to different levels of harvest intensity. For example, comparing phenotypic trait distributions in populations from areas with long-term fishing pressure compared to those with minimal harvest could help identify outcomes of selection in the field.

Further understanding of social and environmental context is also key to uncovering mechanisms underpinning fishing selection. Such questions would be especially suited to lab-based experimental approaches. For example, future research should expand on the findings of this thesis by examining how acclimation versus acute changes in environmental factors can modulate relationships between phenotype and capture. Lastly, differences in traits between individuals and groups should also be considered as the findings from this thesis suggest that behavioural outcomes may depend on group identity and structure. Since ornamental species are often highly social, future work should explore how social context influences vulnerability to capture, and whether group-level traits themselves might be subject to selection. This could involve examining group dynamics under different fishing scenarios or testing whether groups made up of individuals with different traits, or groups with particular leaders have different vulnerabilities to capture.

## 6.5 Conclusion

This thesis provides the first exploration of how behavioural, physiological, and morphological traits are linked to capture in the ornamental fishing trade. Using lab simulations, field observations, and across different environmental contexts, this thesis shows that capture is not random but trait-based, with consistent patterns across species and gear types. These findings provide an important foundation towards understanding the potential of selection in ornamental fisheries, that ornamental fishing can exert selective pressures similar to those documented in larger commercial and recreational fisheries. This thesis also highlights the potential for gear-based selectivity in the ornamental fishing trade as active and passive gears tend to capture individuals with different behavioural traits, which may drive divergent selection if used consistently. Importantly, trait expression was found to be environmental variables, namely temperature, suggesting that environmental change could alter the direction and strength of selection in these systems. Finally, the role of group dynamics and collective behaviour emerged as an important factor to consider. Behaviour varied not only between individuals, but also between groups, with group composition influencing behaviours relevant to capture. This raises important questions about how selection operates in social species, where individual traits may be masked or amplified by group-level processes. In summary, this thesis contributes a novel perspective on fishing-induced selection by focusing on a previously overlooked system and broadens our understanding of how artisanal fisheries can shape wild populations.

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# Appendices

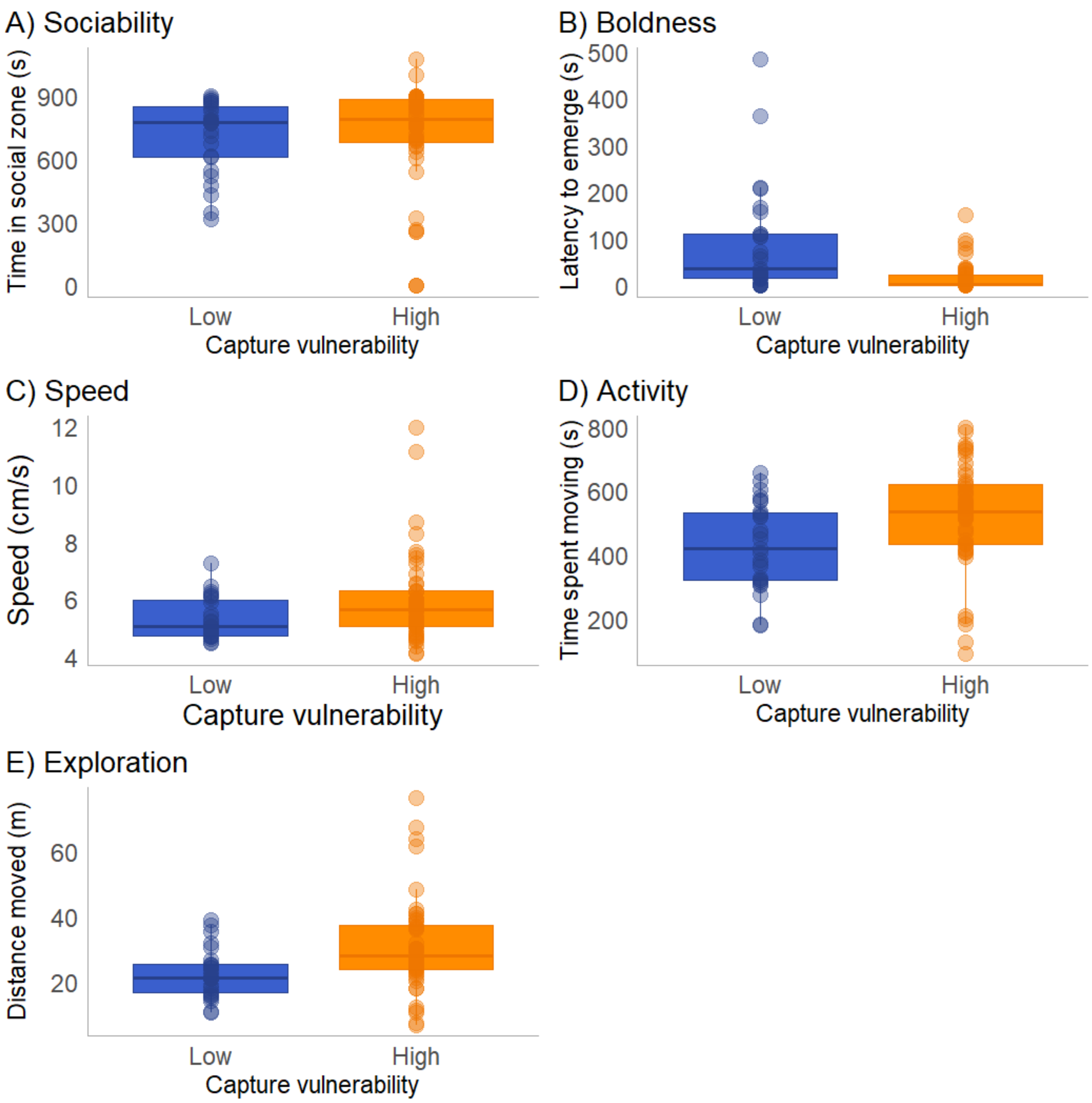
## Supplementary Materials: Chapter 2

**Supplementary Table 2.1)** Model outputs for the vulnerability assays.

| Model | Trait | Term | Estimate | SE | *t* | *P* |
|---|---|---|---|---|---|---|
| 1 | percentage caught | intercept | 65.54 | 4.54 | 14.45 | **<0.001** |
| | | fishing round 2 | -16.61 | 6.80 | -2.44 | **0.021** |
| | | fishing round 3 | -22.69 | 8.49 | -2.44 | **0.012** |
| 2 | entry latency | fishing round 2 | 27.18 | 55.81 | 0.49 | 0.630 |
| | | fishing round 3 | 65.59 | 72.60 | 0.90 | 0.374 |
| | | temperature | 122.03 | 138.32 | 0.88 | 0.385 |

**Supplementary Table 2.2)** Final model outputs for the impacts of behavioural traits on capture vulnerability.

| Model | Trait | Term | Estimate | SE | *z* | *P* |
|---|---|---|---|---|---|---|
| 1 | capture vulnerability | intercept | -0.62 | 0.82 | -0.755 | 0.450 |
| | | exploration | 0.07 | 0.03 | 2.429 | **0.015** |
| | | boldness | -0.02 | 0.007 | -2.812 | **0.004** |
| 2 | capture vulnerability | intercept | -4.56 | 2.41 | -1.890 | 0.059 |
| | | activity | 0.004 | 0.002 | 2.091 | **0.036** |
| | | speed | 0.71 | 0.37 | 1.914 | 0.056 |
| | | boldness | -0.02 | 0.007 | -2.837 | **0.004** |



**Supplementary Figure 2.1** Comparison of behavioural traits between individuals with high and low vulnerability to capture: A) sociability, using time within a social zone as a proxy; B) boldness, using latency to emerge from acclimation zone as a proxy; C) speed, calculated as distance over time; D) activity, using time spent moving during a trial as a proxy; and E) exploration, using distance covered within the arena as a proxy. Each data point represents a focal fish during a trial.

**Supplementary Table 2.3)** Model outputs for the impact of PCA scores on capture vulnerability.

| **Trait** | **Term** | **Estimate** | **SE** | *z* | ***P*** |
|---|---|---|---|---|---|
| capture vulnerability | intercept | 0.74 | 0.28 | 2.63 | **0.009** |
| | PC1 | 0.68 | 0.25 | 2.74 | **0.006** |
| | PC2 | 0.24 | 0.27 | 0.89 | 0.375 |

**Supplementary Table 2.4)** Model output for the impact of body mass and fatigue on capture vulnerability.

| Trait | Term | Estimate | SE | *z* | *P* |
|---|---|---|---|---|---|
| capture vulnerability | intercept | 5.28 | 1.39 | 3.80 | **<0.001** |
|  | mass | -7.50 | 2.97 | -2.52 | **0.012** |
|  | fatigue | -0.03 | 0.01 | -2.24 | **0.025** |
|  | mass: fatigue | -0.07 | 0.14 | -0.50 | 0.620 |

## Supplementary Materials: Chapter 3

**Supplementary Table 3.1)** Environmental data obtained during fish collections.

| Date | Number | Gear | Water temperature (°C) | Air temperature (°C) | pH | Oxygen saturation (mg / l) | Oxygen saturation (%) |
|---|---|---|---|---|---|---|---|
| 25/09/2022 | 1 | Net | 26.8 | 27.6 | 4.5 | 1.6 | 20.3 |
| 25/09/2022 | 1 | Trap | 27.6 | 33.6 | 4.6 | 2.2 | 28.7 |
| 25/09/2022 | 2 | Net | 27.7 | 30.3 | 4.5 | 1.6 | 20.6 |
| 25/09/2022 | 3 | Net | 27.7 | 29.8 | 4.4 | 1.6 | 19.9 |
| 25/09/2022 | 4 | Net | 27.9 | 29.8 | 4.5 | 1.4 | 18.3 |
| 27/09/2022 | 1 | Trap | 28.2 | 35.8 | 4.5 | 3.6 | 46.5 |
| 27/09/2022 | 1 | Net | 28.2 | 35.8 | 4.5 | 3.6 | 46.5 |
| 27/09/2022 | 2 | Trap | 28.4 | 34.7 | 4.5 | 3.8 | 48.7 |
| 27/09/2022 | 2 | Net | 28.4 | 34.7 | 4.5 | 3.8 | 48.7 |
| 27/09/2022 | 3 | Trap | 29.3 | 35.4 | 4.5 | 3.7 | 49.7 |
| 27/09/2022 | 3 | Net | 29.3 | 35.4 | 4.5 | 3.7 | 49.7 |
| 27/09/2022 | 4 | Trap | 28.5 | 36.8 | 4.5 | 3.8 | 48.8 |
| 27/09/2022 | 4 | Net | 28.5 | 36.8 | 4.5 | 3.8 | 48.8 |
| 28/09/2022 | 1 | Trap | 28.4 | 30.9 | 4.9 | 3.5 | 45.0 |
| 28/09/2022 | 2 | Trap | 29.0 | 31.0 | 4.7 | 2.8 | 36.0 |
| 28/09/2022 | 3 | Trap | 28.0 | 28.7 | 4.4 | 2.9 | 37.4 |
| 28/09/2022 | 4 | Trap | 28.0 | 28.7 | 4.5 | 3.1 | 39.9 |

**Supplementary Table 3.2)** Model outputs for constant acceleration test data. Mode outputs include results from the initial and final models.

| Trait | Model | Term | Estimate | SE | *t* | *P* |
|---|---|---|---|---|---|---|
| Maximum Swimming Speed | Initial | Intercept | -8.49 | 22.32 | -0.38 | 0.704 |
|  |  | Net | -9.07 | 34.07 | -0.27 | 0.791 |
|  |  | Temperature | 0.88 | 0.81 | 1.10 | 0.276 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
|  |  | Mean standard length | 0.89 | 3.46 | 0.26 | 0.798 |
|  |  | Net: Temperature | 0.39 | 1.28 | 0.31 | 0.76 |
|  | Final | Intercept | -9.86 | 16.55 | -0.60 | 0.553 |
|  |  | Net | -1.25 | 0.47 | -2.68 | **0.008** |
|  |  | Temperature | 1.03 | 0.62 | 1.66 | 0.099 |
| Time Until Exhaustion | Initial | Intercept | -2539.12 | 1838.96 | -1.38 | 0.170 |
|  |  | Net | -118.39 | 2806.36 | -0.04 | 0.966 |
|  |  | Temperature | 84.36 | 66.52 | 1.27 | 0.207 |
|  |  | Mean standard length | 1058.44 | 284.81 | 3.72 | **<0.001** |
|  |  | Trap: Temperature | 8.23 | 105.19 | 0.08 | 0.938 |
|  | Final | Intercept | -244.47 | 411.46 | -0.59 | 0.554 |
|  |  | Net | 96.39 | 51.93 | 1.86 | 0.066 |
|  |  | Mean standard length | 1028.13 | 285.36 | 3.60 | **<0.001** |

**Supplementary Table 3.3)** Model outputs for maze data. Mode outputs include results from the initial and final models.

| **Trait** | **Level** | **Model** | **Term** | **Estimate** | **SE** | ***t*** | ***P*** |
|---|---|---|---|---|---|---|---|
| Risk-taking | Individual | Initial | Intercept | 901.04 | 411.29 | 2.19 | 0.036 |
|  |  |  | Trap | -753.83 | 572.84 | -1.32 | 0.198 |
|  |  |  | Temperature | -32.44 | 15.75 | -2.06 | 0.479 |
|  |  |  | Average total length | -5.40 | 31.72 | -0.17 | 0.866 |
|  |  |  | Trap: Temperature | 27.95 | 21.87 | 1.28 | 0.211 |
|  |  | Final | Intercept | 43.11 | 6.82 | 6.32 | **<0.001** |
|  |  |  | Trap | -23.61 | 9.65 | -2.45 | **0.020** |
|  | Group | Initial | Intercept | 440.83 | 473.56 | 0.93 | 0.359 |
|  |  |  | Trap | -1035.58 | 659.57 | -1.57 | 0.127 |
|  |  |  | Temperature | -16.21 | 18.13 | -0.90 | 0.378 |
|  |  |  | Average total length | 26.39 | 36.53 | 0.72 | 0.475 |
|  |  |  | Trap: Temperature | 38.79 | 25.18 | 1.54 | 0.134 |
|  |  | Final | Intercept | 62.56 | 7.70 | 8.12 | **<0.001** |
| Maze Completion | Individual |  | Intercept | -216.09 | 820.15 | -0.26 | 0.794 |
|  |  |  | Trap | 21.99 | 92.27 | 0.24 | 0.813 |
|  |  |  | Temperature | 14.05 | 30.10 | 0.47 | 0.645 |
|  |  |  | Average total length | -14.33 | 81.90 | -0.18 | 0.862 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
|  |  |  | Risk-taking (individual) | -0.38 | 0.44 | -0.87 | 0.392 |
|  |  |  | Cohesion | -0.27 | 0.89 | -0.30 | 0.766 |
|  |  |  | Trap: Cohesion | -0.38 | 1.49 | -0.25 | 0.802 |
|  |  | Final | Intercept | 116.84 | 16.11 | 7.25 | **<0.001** |
|  |  |  | Risk-taking (individual) | -0.52 | 0.36 | -1.48 | 0.149 |
|  | Group | Initial | Intercept | 876.73 | 3381.71 | 0.26 | 0.797 |
|  |  |  | Net | 627.43 | 337.07 | 1.86 | 0.073 |
|  |  |  | Temperature | -46.54 | 121.00 | -0.39 | 0.703 |
|  |  |  | Average total length | 55.70 | 328.77 | 0.17 | 0.867 |
|  |  |  | Risk-taking (group) | 1.45 | 1.51 | 0.96 | 0.345 |
|  |  |  | Cohesion | 9.40 | 4.56 | 2.06 | **0.049** |
|  |  |  | Net: cohesion | -13.78 | 5.59 | -2.46 | **0.020** |
|  |  | Final | Intercept | -159.53 | 196.10 | -0.81 | 0.422 |
|  |  |  | Net | 660.39 | 295.55 | 2.23 | **0.032** |
|  |  |  | Cohesion | 9.11 | 3.65 | 2.50 | **0.018** |
|  |  |  | Net: Cohesion | -13.92 | 4.96 | -2.81 | **0.008** |
| Cohesion | Group | Initial | Intercept | 440.23 | 185.91 | 2.37 | **0.025** |
|  |  |  | Net | 11.65 | 6.74 | 1.73 | 0.094 |
|  |  |  | Temperature | -13.33 | 7.05 | -1.89 | 0.069 |
|  |  |  | Average total length | -18.96 | 20.00 | -0.95 | 0.352 |
|  |  |  | Risk-taking (group) | -0.13 | 0.10 | -1.33 | 0.194 |
|  |  |  | Completion (group) | 0.02 | 0.01 | 0.21 | 0.836 |
|  |  |  | Net Temperature | 21.78 | 16.11 | 1.35 | 0.187 |
|  |  | Final | Intercept | 434.42 | 175.88 | 2.47 | **0.019** |
|  |  |  | Net | 13.59 | 6.01 | 2.26 | **0.031** |
|  |  |  | Temperature | -14.39 | 6.72 | -2.14 | **0.040** |
|  |  |  | Risk-taking (group) | -0.13 | 0.09 | -1.48 | 0.150 |

**Supplementary Table 3.4)** Model outputs for open field and novel object data. Mode outputs include results from the initial and final models.

| **Trait** | **Model** | **Term** | **Estimate** | **SE** | ***df*** | ***t*** | ***P*** |
|---|---|---|---|---|---|---|---|
| Speed | Initial | Intercept | -25.91 | 11.59 | 66.91 | -2.24 | **0.029** |
|  |  | Net | 0.89 | 0.55 | 66.90 | 1.62 | 0.110 |
|  |  | Open Field | 0.79 | 0.53 | 66.94 | 1.49 | 0.140 |

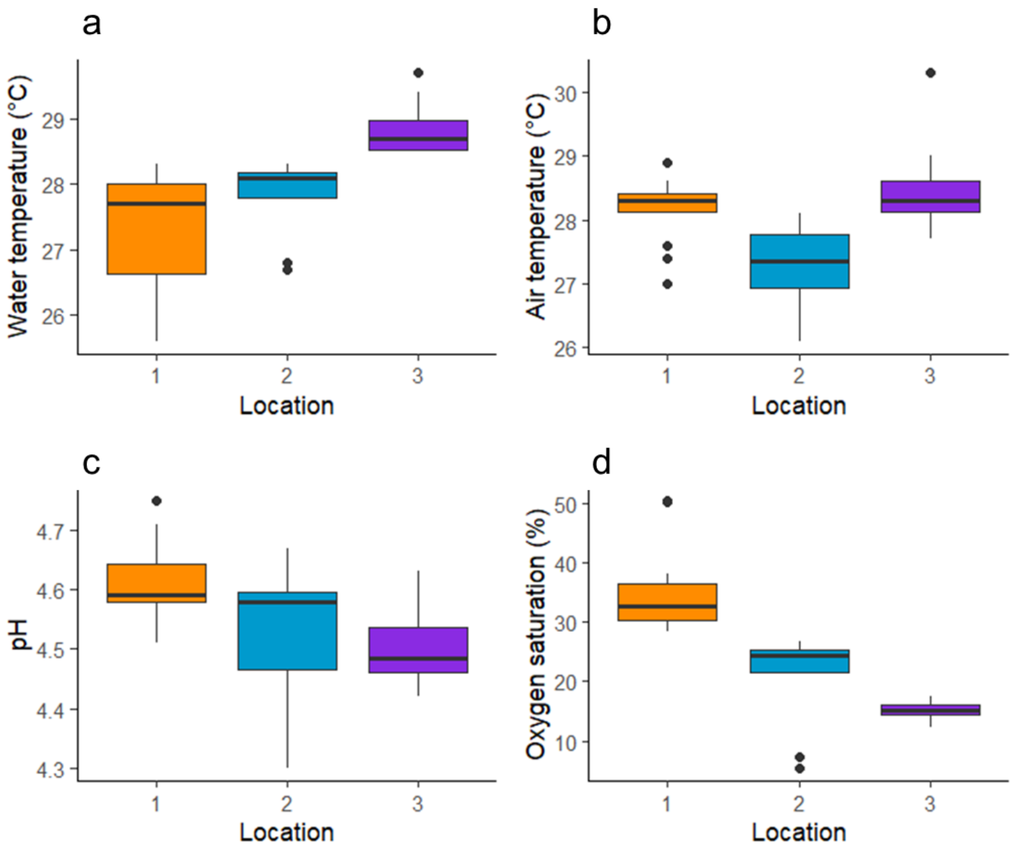
| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | Temperature | 1.14 | 0.44 | 66.91 | 2.60 | **0.012** |
| | | Net: Open Field | -0.05 | 0.77 | 66.95 | -0.07 | 0.946 |
| | Final | Intercept | -25.90 | 11.50 | 67.91 | -2.25 | **0.028** |
| | | Net | 0.86 | 0.39 | 67.94 | 2.23 | **0.029** |
| | | Open Field | 0.77 | 0.38 | 67.94 | 2.01 | **0.049** |
| | | Temperature | 1.14 | 0.44 | 67.91 | 2.62 | **0.011** |
| Average Neighbour Distance | Initial | Intercept | -1.67 | 17.80 | 66.76 | -0.09 | 0.925 |
| | | Net | -1.49 | 0.84 | 66.74 | -1.77 | 0.081 |
| | | Open Field | 0.43 | 0.82 | 66.83 | 0.53 | 0.601 |
| | | Temperature | 0.41 | 0.68 | 66.76 | 0.61 | 0.544 |
| | | Net: Open Field | 0.54 | 1.19 | 66.84 | 0.45 | 0.653 |
| | Final | Intercept | 9.41 | 0.41 | 69.78 | 23.20 | **<0.001** |
| | | Net | -1.27 | 0.59 | 69.79 | -2.15 | **0.035** |
| Risk-taking $_{\mathrm{A}}$ | Initial | Intercept | -25.15 | 27.05 | 66.93 | -0.93 | 0.356 |
| | | Net | 1.10 | 1.28 | 66.92 | 0.86 | 0.393 |
| | | Open Field | -1.52 | 1.24 | 66.96 | -1.22 | 0.227 |
| | | Temperature | 1.70 | 1.03 | 66.93 | 1.65 | 0.103 |
| | | Net: Open Field | 0.55 | 1.81 | 66.96 | 0.31 | 0.761 |
| | Final | Intercept | 19.30 | 0.46 | 70.96 | 42.04 | **<0.001** |
| Risk-taking $_{\mathrm{NO}}$ | Initial | Intercept | -28.46 | 63.41 | 32.99 | -0.45 | 0.657 |
| | | Net | 1.55 | 2.13 | 33.00 | 0.73 | 0.473 |
| | | Temperature | 1.87 | 2.41 | 32.99 | 0.77 | 0.445 |
| | Final | Intercept | 21.24 | 1.04 | 35.00 | 20.36 | **<0.001** |
| Exploration (Open Field) | Initial | Intercept | -6022.68 | 4663.73 | 32.96 | -1.29 | 0.206 |
| | | Net | 206.15 | 156.74 | 32.97 | 1.32 | 0.198 |
| | | Temperature | 271.07 | 177.32 | 32.96 | 1.53 | 0.136 |
| | Final | Intercept | 1190.21 | 79.66 | 35 | 14.94 | **<0.001** |
| Exploration (Novel Object) | Initial | Intercept | -12318.41 | 5735.53 | 32.98 | -2.15 | **0.039** |
| | | Net | 362.83 | 192.77 | 32.99 | 1.88 | 0.069 |
| | | Temperature | 519.65 | 218.07 | 32.98 | 2.38 | **0.023** |
| | Final | Intercept | -12318.4 | 5735.53 | 32.98 | -2.15 | **0.039** |
| | | Net | 362.83 | 192.77 | 32.99 | 1.88 | 0.069 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | Temperature | 519.65 | 218.07 | 32.98 | 2.38 | **0.023** |

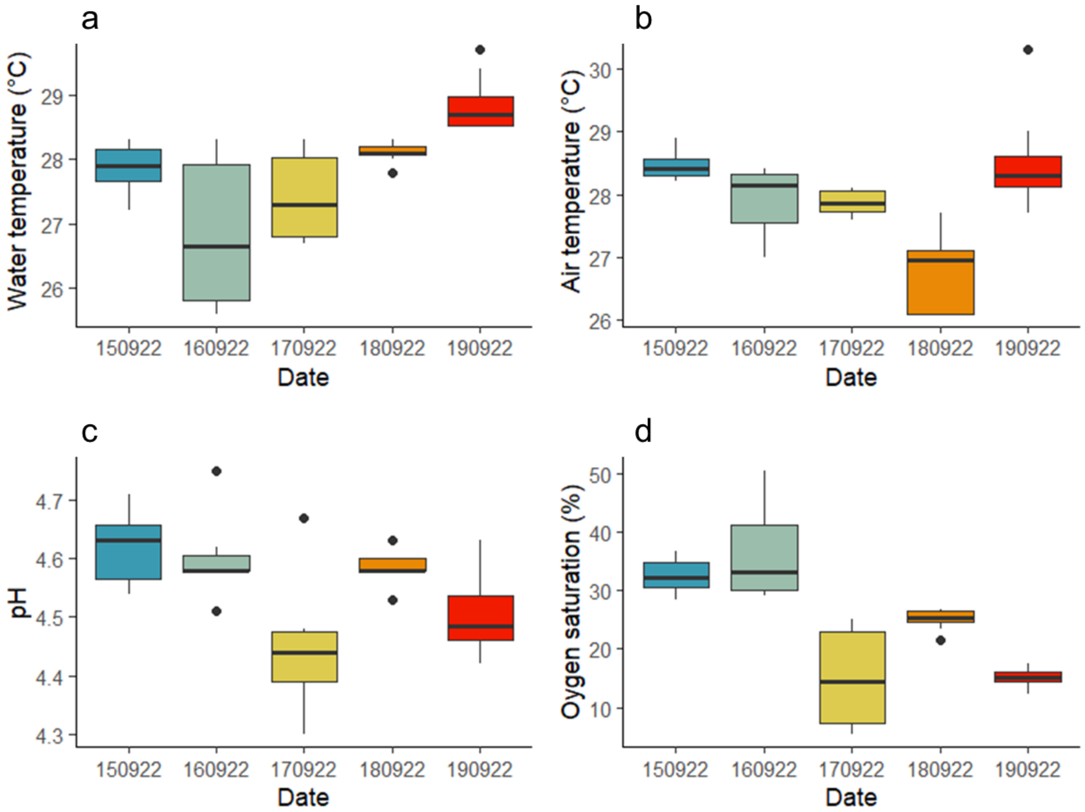
# Supplementary Materials: Chapter 4

**Supplementary Table 4.1)** Fieldwork schedule with number of days fished at each site.

| Date | Site | Number of days fishing in site |
|---|---|---|
| 15/09/2022 | 1 | 1 |
| 16/09/2022 | 1 | 2 |
| 17/09/2022 | 2 | 1 |
| 18/09/2022 | 2 | 2 |
| 19/09/2022 | 3 | 1 |



**Supplementary Figure 4.1)** Boxplots for environmental data across the three field sites: a) water temperature; b) air temperature; c) pH; and d) oxygen saturation.

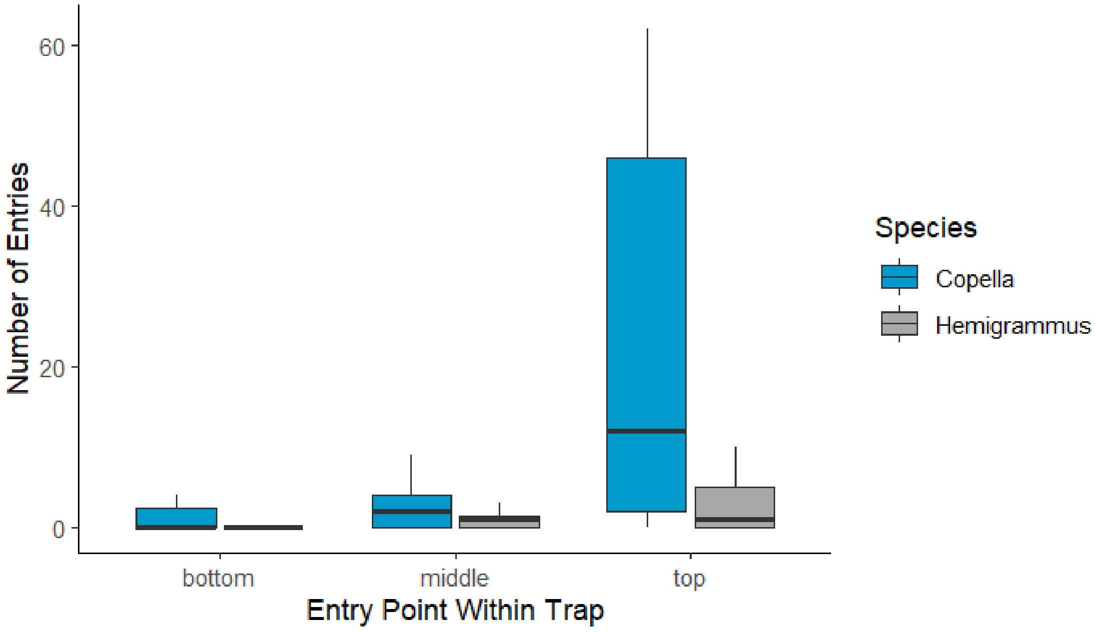


**Supplementary Figure 4.2)** Boxplots for environmental data on different survey dates: a) water temperature; b) air temperature; c) pH; and d) oxygen saturation. Data points beyond the range of the boxes represent outliers.

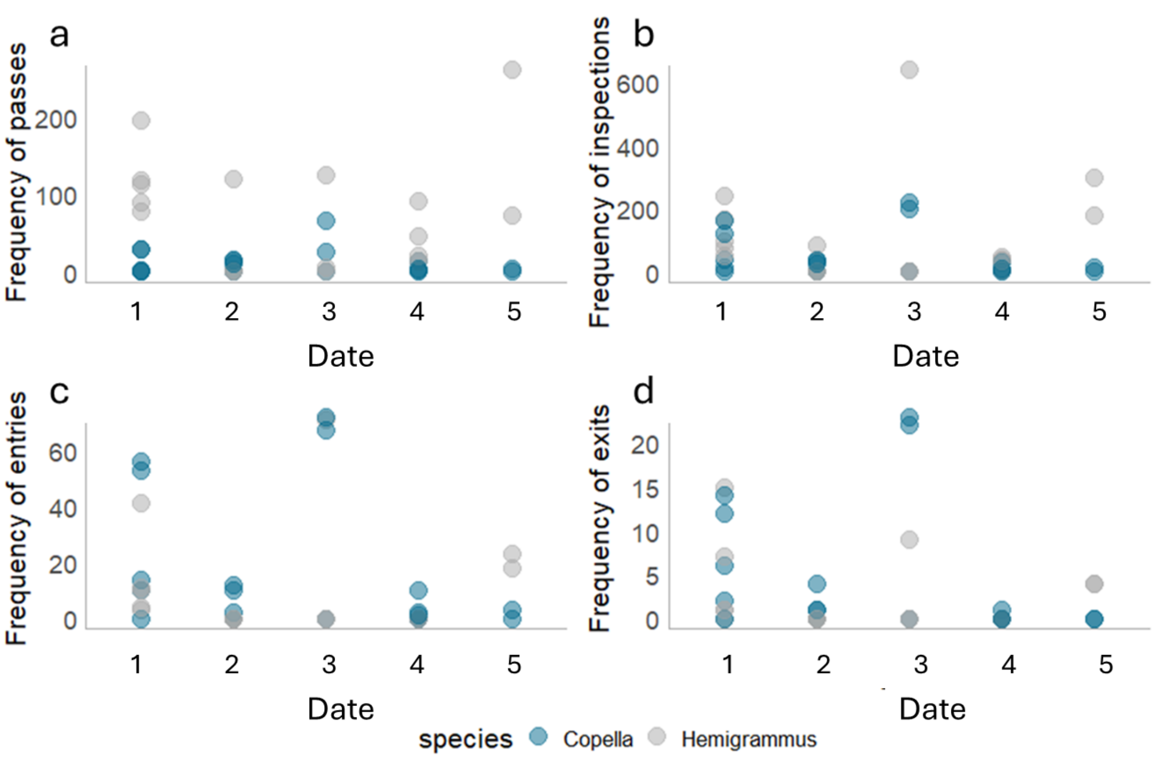
**Supplementary Table 4.2)** Taxonomic list of all identified genus and species visible within the field of view for each video trial.

| Date | Site | Trial | Genus/ Species |
|---|---|---|---|
| 15/09/2022 | 1 | 1 | *Copella nattereri, Hemigrammus sp., Nannostomus eques* |
| 15/09/2022 | 1 | 3 | *Apistogramma sp., Copella nattereri, Hemigrammus sp.* |
| 15/09/2022 | 1 | 4 | *Copella nattereri, Hemigrammus sp.* |
| 15/09/2022 | 1 | 5 | *Copella nattereri, Hemigrammus sp.* |
| 15/09/2022 | 1 | 6 | *Apistogramma sp., Copella nattereri, Hemigrammus sp., Bryconops sp. (larval)* |
| 16/09/2022 | 1 | 1 | *Apistogramma sp., Mesonauta insignis* |
| 16/09/2022 | 1 | 2 | *Copella nattereri, Bryconops sp. (larval)* |
| 16/09/2022 | 1 | 3 | *Copella nattereri, Hemigrammus sp., Nannostomus eques.* |
| 16/09/2022 | 1 | 5 | *Apistogramma sp., Copella nattereri, Bryconops sp. (larval), Mesonauta insignis* |

| | | | |
|---|---|---|---|
| 17/09/2022 | 2 | 1 | *Bryconops sp., Copella nattereri, Hemigrammus sp., Hemigrammus sp. 2., Nannostomus eques* |
| 17/09/2022 | 2 | 3 | *Copella nattereri* |
| 17/09/2022 | 2 | 5 | *Copella nattereri, Hemigrammus sp.* |
| 18/09/2022 | 2 | 1 | *Copella nattereri, Hemigrammus sp.* |
| 18/09/2022 | 2 | 3 | *Copella nattereri, Hemigrammus sp.* |
| 18/09/2022 | 2 | 5 | *Bryconops sp., Hemigrammus sp., Nannostomus eques* |
| 18/09/2022 | 2 | 7 | *Bryconops sp., Copella nattereri, Hemigrammus sp.* |
| 19/09/2022 | 3 | 1 | *Apistogramma sp., Hemigrammus sp., Nannostomus eques* |
| 19/09/2022 | 3 | 5 | *Hemigrammus sp., Moenkhausia cotinho, Nannostomus eques* |



**Supplementary Figure 4.3)** Number of entries within different locations of the trap for both species using data from high visibility videos



**Supplementary Figure 4.4)** The relationship between date of capture and the frequency of: a) passes; b) inspections; c) entries; and d) exits. As dates were successive between the 15th-19th of September, these are represented by a number between 1-5 for simplicity. Each data point represents the frequency of behaviours observed within a trial.

**Supplementary Table 4.3)** Summary of factors contributing to the frequency of observed behaviours (passes, inspections, entries and exits) and the number of individuals caught (entries-exits). Each model shown is the final model determined via stepwise model selection (as described in methods). The multiple R-squared (*$r^2_m$)* and adjusted R-squared (*$r^2_a$)* are also shown for each model. The threshold level of significance for p values is given at 0.05 and significant values are displayed in bold.

| **Trait** | **Term** | **Estimate** | **Std. Error** | **t value** | **p value** | **$r^2$m** | **$r^2$a** |
|---|---|---|---|---|---|---|---|
| **Pass frequency** | | | | | | 0.456 | 0.344 |
| | Intercept | 57.96 | 24.90 | 2.33 | **0.027** | | |
| | Date (16/09/2022) | -51.96 | 24.15 | -2.15 | **0.040** | | |
| | Date (17/09/2022) | -33.37 | 26.03 | -1.28 | 0.210 | | |
| | Date (18/09/2022) | -40.07 | 23.69 | -1.69 | 0.101 | | |
| | Date (19/09/2022) | 14.04 | 29.75 | 0.47 | 0.640 | | |
| | Trial | -6.51 | 4.57 | -1.42 | 0.165 | | |
| | Species (Hemigrammus) | 63.56 | 16.63 | 3.82 | **<0.001** | | |
| **Inspection frequency** | | | | | | 0.273 | 0.152 |
| | Intercept | 67.07 | 41.28 | 1.62 | 0.115 | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Date (16/09/2022) | -73.03 | 54.78 | -1.33 | 0.193 | | |
| | Date (17/09/2022) | 81.10 | 59.64 | 1.36 | 0.184 | | |
| | Date (18/09/2022) | -75.78 | 54.78 | -1.38 | 0.177 | | |
| | Date (19/09/2022) | 24.85 | 68.33 | 0.36 | 0.719 | | |
| | Species (Hemigrammus) | 57.67 | 38.50 | 1.50 | 0.145 | | |
| **Entry frequency** | | | | | | 0.303 | 0.213 |
| | Intercept | 20.20 | 6.25 | 3.24 | **0.003** | | |
| | Date (16/09/2022) | -17.20 | 9.37 | -1.84 | 0.076 | | |
| | Date (17/09/2022) | 14.80 | 10.20 | 1.45 | 0.157 | | |
| | Date (18/09/2022) | -18.58 | 9.37 | -1.98 | 0.056 | | |
| | Date (19/09/2022) | -9.20 | 11.68 | -0.79 | 0.437 | | |
| **Exit frequency** | | | | | | 0.291 | 0.144 |
| | Intercept | -59.85 | 154.77 | -0.39 | 0.702 | | |
| | Date (16/09/2022) | -76.99 | 55.23 | -1.39 | 0.174 | | |
| | Date (17/09/2022) | 141.25 | 92.65 | 1.53 | 0.138 | | |
| | Date (18/09/2022) | -46.92 | 64.64 | -0.73 | 0.474 | | |
| | Date (19/09/2022) | 95.25 | 107.49 | 0.89 | 0.383 | | |
| | Species (Hemigrammus) | 57.67 | 38.68 | 1.49 | 0.147 | | |
| | Oxygen saturation (%) | 3.97 | 4.66 | 0.85 | 0.402 | | |
| **Caught** | | | | | | 0.287 | 0.195 |
| | Intercept | 14.40 | 4.75 | 3.04 | 0.005 | | |
| | Date (16/09/2022) | -12.28 | 7.12 | -1.73 | 0.095 | | |
| | Date (17/09/2022) | 11.60 | 7.75 | 1.50 | 0.145 | | |
| | Date (18/09/2022) | -12.90 | 7.12 | -1.81 | 0.080 | | |
| | Date (19/09/2022) | -5.40 | 8.88 | -0.61 | 0.548 | | |

**Supplementary Table 4.4)** Summary of factors contributing to the inspection latency and entry latency. Each model shown is the final model determined via stepwise model selection (as described in methods). The multiple R-squared ($r^2_m$) and adjusted R-squared ($r^2_a$) are also shown for each model. The threshold level of significance for p values is given at 0.05 and significant values are displayed in bold.

| **Trait** | **Term** | **Estimate** | **Std. Error** | **t value** | **p value** | **$r^2$m** | **$r^2$a** |
|---|---|---|---|---|---|---|---|
| **Inspection latency** | | | | | | 0.253 | 0.225 |
| | Intercept | 3385.10 | 1090.48 | 3.10 | **0.005** | | |
| | Water temperature | -116.14 | 39.11 | -2.97 | **0.006** | | |
| Entry latency | | -33.37 | 26.03 | -1.28 | 0.210 | | |
| | Intercept | 276.83 | 62.48 | 4.43 | **<0.001** | | |

**Supplementary Table 4.5)** Summary of factors contributing to the average rate of inspection and entry. Each model shown is the final model determined via stepwise model selection (as described in methods). The multiple R-squared (r2m) and adjusted R-squared (r2a) are also shown for each model. The threshold level of significance for p values is given at 0.05 and significant values are displayed in bold.

| **Trait** | **Term** | **Estimate** | **Std. Error** | **t value** | **p value** | **$r^2$m** | **$r^2$a** |
|---|---|---|---|---|---|---|---|
| **Average rate of inspection** | | | | | | 0.464 | 0.311 |
| | Intercept | -0.16 | 0.08 | -1.94 | 0.065 | | |
| | Date (16/09/2022) | -0.01 | 0.04 | -0.30 | 0.766 | | |
| | Date (17/09/2022) | 0.16 | 0.05 | 3.06 | **0.006** | | |
| | Date (18/09/2022) | 0.01 | 0.03 | 0.35 | 0.731 | | |
| | Date (19/09/2022) | 0.14 | 0.06 | 2.42 | **0.025** | | |
| | Species (Hemigrammus) | 0.06 | 0.02 | 2.45 | **0.023** | | |
| | Oxygen Saturation (%) | 0.006 | 0.002 | 2.51 | **0.021** | | |
| **Average rate of entry** | | | | | | 0.586 | 0.482 |
| | Intercept | 0.03 | 0.003 | 9.17 | **<0.001** | | |
| | Date (16/09/2022) | -0.006 | 0.006 | -1.04 | 0.313 | | |
| | Date (17/09/2022) | 0.02 | 0.006 | 4.15 | **<0.001** | | |
| | Date (18/09/2022) | -0.001 | 0.006 | -0.24 | 0.814 | | |

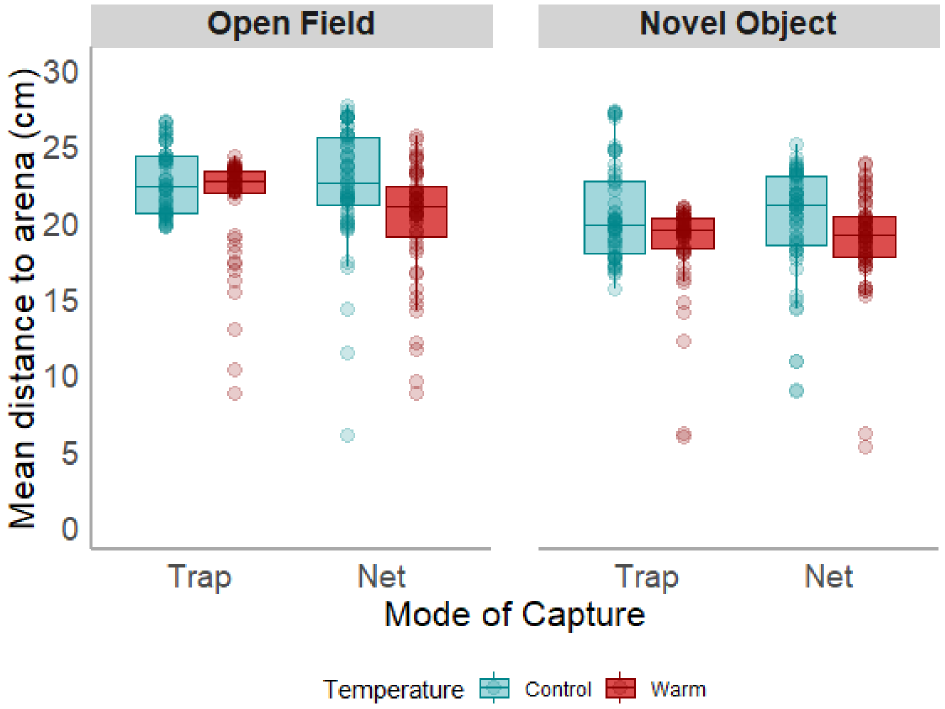
| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Date (19/09/2022) | 0.004 | 0.006 | 0.66 | 0.522 | | |

**Supplementary Table 4.6)** Summary of factors contributing to the coefficient of dispersion. Each model shown is the final model determined via stepwise model selection (as described in methods). The multiple R-squared (r2m) and adjusted R-squared (r2a) are also shown for each model. The threshold level of significance for p values is given at 0.05 and significant values are displayed in bold.

| **Trait** | **Term** | **Estimate** | **Std. Error** | **t value** | **p value** | **$r^2$m** | **$r^2$a** |
|---|---|---|---|---|---|---|---|
| **CD pass** | | | | | | 0.676 | 0.401 |
| | Intercept | 6.54 | 4.95 | 1.32 | 0.209 | | |
| | Date (16/09/2022) | -0.35 | 0.42 | -0.84 | 0.416 | | |
| | Date (17/09/2022) | 0.98 | 0.41 | 2.37 | **0.034** | | |
| | Date (18/09/2022) | 0.08 | 0.41 | 0.20 | 0.845 | | |
| | Date (19/09/2022) | -0.14 | 0.51 | -0.27 | 0.791 | | |
| | Species (Hemigrammus) | -11.62 | 7.25 | -1.61 | 0.133 | | |
| | Water temperature | -0.23 | 0.18 | -1.27 | 0.226 | | |
| | 16/09/2022 * Hemigrammus | -0.05 | 0.57 | -0.09 | 0.931 | | |
| | 17/09/2022 * Hemigrammus | -1.14 | 0.56 | -2.06 | 0.060 | | |
| | 18/09/2022 * Hemigrammus | -0.38 | 0.49 | -0.78 | 0.448 | | |
| | Hemigrammus * Water temperature | 0.56 | 0.62 | 0.91 | 0.377 | | |
| **CD inspect** | | | | | | 0.409 | 0.202 |
| | Intercept | 3.19 | 3.42 | 0.93 | 0.361 | | |
| | Date (16/09/2022) | -0.005 | 0.22 | -0.02 | 0.983 | | |
| | Date (17/09/2022) | 0.26 | 0.19 | 1.38 | 0.184 | | |
| | Date (18/09/2022) | -0.30 | 0.16 | -1.86 | 0.078 | | |
| | Date (19/09/2022) | -0.03 | 0.23 | -0.13 | 0.896 | | |
| | Species (Hemigrammus) | -16.11 | 7.06 | -2.28 | **0.034** | | |
| | Water temperature | -0.10 | 0.12 | -0.82 | 0.43 | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | Hemigrammus * Water temperature | 0.58 | 0.25 | 2.3 | **0.032** | | |
| **CD enter** | | | | | | 0.473 | 0.579 |
| | Intercept | 0.10 | 0.13 | 0.76 | 0.464 | | |
| | Location (tabazinho) | 0.02 | 0.15 | 0.16 | 0.87 | | |
| | Location (yacaremiri) | -0.10 | 0.19 | -0.54 | 0.602 | | |
| | Date (16/09/2022) | -0.06 | 0.10 | -0.63 | 0.545 | | |
| | Date (17/09/2022) | 0.30 | 0.16 | 1.85 | 0.092 | | |
| | Species (Hemigrammus) | 0.36 | 0.16 | 2.22 | **0.049** | | |
| | Water temperature | -0.23 | 0.18 | -1.27 | 0.226 | | |
| | Tabazinho * Hemigrammus | -0.35 | 0.18 | -1.88 | 0.087 | | |
| | Yacaremiri * Hemigrammus | -0.07 | 0.23 | -0.31 | 0.765 | | |
| **CD exit** | | | | | | 0.978 | 0.940 |
| | Intercept | -1.11 | 0.53 | -2.09 | 0.105 | | |
| | Date (16/09/2022) | 0.04 | 0.04 | 1.13 | 0.323 | | |
| | Date (17/09/2022) | 0.13 | 0.03 | 4.67 | **0.010** | | |
| | Date (19/09/2022) | -0.20 | 0.03 | -6.13 | **0.004** | | |
| | Species (Hemigrammus) | -8.48 | 1.84 | -4.61 | **0.010** | | |
| | Water temperature | 0.04 | 0.02 | 1.77 | 0.152 | | |
| | Oxygen saturation (%) | 0.003 | 0.002 | 1.44 | 0.224 | | |
| | Hemigrammus * Water temperature | 0.31 | 0.07 | 4.66 | **0.010** | | |

## Supplementary Materials: Chapter 5



**Supplementary Figure 5.1)** Differences in risk-taking between fish caught by different gears and exposed to an elevated temperature during open field and novel object tests. Each data point represents an individual. Each box shows the interquartile range (25th to 75th percentile), with the middle horizontal line representing the median. Whiskers represent the most extreme values within 1.5 times the interquartile range from the lower and upper quartiles. Data points outside of the range of the whiskers are shown as outliers. Horizontal lines and asterisks indicate statistically significant differences between variables based on model outputs. Significance levels are shown as: p < 0.05 (*), p < 0.01 (**), p < 0.001 (***), p < 0.0001 (****).

**Supplementary Table 5.1)** Environmental variables collected during fish collection.

| Date | Trial | Gear | Air temperature (°C) | Water temperature (°C) | pH | Oxygen saturation (%) |
|---|---|---|---|---|---|---|
| 150922 | 1 | rapiché | 27.1 | 26.2 | 4.40 | 9.8 |
| 150922 | 2 | rapiché | 27.5 | 26.6 | 4.36 | 20.6 |
| 150922 | 3 | rapiché | 26.6 | 25.6 | 4.67 | 45.5 |
| 150922 | 1 | cacuri | 28.3 | 28 | 4.65 | 30.6 |
| 150922 | 2 | cacuri | 28.3 | 27.2 | 4.71 | 35.2 |
| 150922 | 3 | cacuri | 28.2 | 28.2 | 4.55 | 36.8 |
| 150922 | 4 | cacuri | 28.5 | 28.3 | 4.61 | 28.4 |
| 150922 | 5 | cacuri | 28.9 | 27.8 | 4.66 | 33.6 |

|  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|
| 150922 | 6 | cacuri | 28.6 | 27.6 | 4.54 | 30.6 |
| 160922 | 1 | cacuri | 27 | 27.9 | 4.75 | 30 |
| 160922 | 2 | cacuri | 27.4 | 25.6 | 4.6 | 38.2 |
| 160922 | 3 | cacuri | 28.2 | 28.3 | 4.58 | 29 |
| 160922 | 4 | cacuri | 28.1 | 28 | 4.58 | 31.7 |
| 160922 | 5 | cacuri | 27.6 | 26.6 | 4.58 | 34.8 |
| 160922 | 6 | cacuri | 28.3 | 26.7 | 4.51 | 30.2 |
| 160922 | 7 | cacuri | 28.4 | 25.8 | 4.58 | 50.1 |
| 160922 | 8 | cacuri | 28.4 | 25.8 | 4.62 | 50.5 |
| 160922 | 1 | rapiché | 26.9 | 27.8 | 4.55 | 29 |
| 160922 | 2 | rapiché | 27.1 | 27 | 4.59 | 25.9 |
| 160922 | 3 | rapiché | 27.1 | 25.8 | 4.52 | 19 |
| 170922 | 1 | cacuri | 28.1 | 27.8 | 4.67 | 23.5 |
| 170922 | 2 | cacuri | 27.9 | 26.8 | 4.38 | 7.3 |
| 170922 | 3 | cacuri | 27.6 | 28.3 | 4.48 | 21.6 |
| 170922 | 4 | cacuri | 27.7 | 26.8 | 4.42 | 7.3 |
| 170922 | 5 | cacuri | 27.8 | 26.7 | 4.3 | 5.4 |
| 170922 | 6 | cacuri | 28.1 | 28.1 | 4.46 | 25.1 |
| 170922 | 1 | rapiché | 27.8 | 28.6 | 4.54 | 20.9 |
| 170922 | 2 | rapiché | 28 | 28.7 | 4.54 | 23 |
| 170922 | 3 | rapiché | 27.9 | 28.8 | 4.53 | 24.5 |
| 180922 | 1 | cacuri | 26.1 | 28.1 | 4.6 | 25.4 |
| 180922 | 2 | cacuri | 26.1 | 28.2 | 4.6 | 26.3 |
| 180922 | 3 | cacuri | 26.1 | 28.1 | 4.58 | 25.2 |
| 180922 | 4 | cacuri | 27.1 | 28.3 | 4.58 | 25 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 180922 | 5 | cacuri | 27.7 | 28.2 | 4.58 | 21.6 |
| 180922 | 6 | cacuri | 27.1 | 28 | 4.58 | 26.7 |
| 180922 | 7 | cacuri | 26.9 | 28.1 | 4.63 | 26.7 |
| 180922 | 8 | cacuri | 27 | 27.8 | 4.53 | 23.4 |
| 180922 | 1 | rapiché | 26.7 | 27.7 | 4.59 | 20 |
| 180922 | 2 | rapiché | 26.2 | 26.4 | 4.59 | 5.9 |
| 180922 | 3 | rapiché | 26.8 | 27.5 | 4.59 | 19.2 |
| 190922 | 1 | cacuri | 30.3 | 28.5 | 4.43 | 14.4 |
| 190922 | 2 | cacuri | 28.3 | 28.6 | 4.55 | 15 |
| 190922 | 1 | rapiché | 27.7 | 29 | 4.52 | 15.6 |
| 190922 | 2 | rapiché | 28 | 29.4 | 4.52 | 16.8 |
| 190922 | 3 | rapiché | 28 | 28.4 | 4.53 | 15.3 |
| 190922 | 3 | cacuri | 29 | 28.6 | 4.46 | 15.6 |
| 190922 | 4 | cacuri | 28.6 | 28.6 | 4.48 | 14.3 |
| 190922 | 5 | cacuri | 27.9 | 28.5 | 4.42 | 14.1 |
| 190922 | 6 | cacuri | 27.7 | 28.8 | 4.49 | 16.5 |
| 190922 | 7 | cacuri | 28.1 | 28.5 | 4.45 | 15.2 |
| 190922 | 8 | cacuri | 27.8 | 28.5 | 4.48 | 14.5 |
| 190922 | 9 | cacuri | 28.2 | 28.9 | 4.63 | 16.2 |
| 190922 | 10 | cacuri | 28.7 | 29.4 | 4.54 | 13.7 |
| 190922 | 11 | cacuri | 28.3 | 29 | 4.49 | 17.4 |
| 190922 | 12 | cacuri | 28.3 | 28.9 | 4.63 | 15.7 |
| 190922 | 13 | cacuri | 28.5 | 29 | 4.53 | 17.4 |
| 190922 | 14 | cacuri | 28.6 | 29.7 | 4.46 | 12.3 |

**Supplementary Table 5.2)** Model outputs for open field tests. Mode outputs include results from the initial and final models.

| **Trait** | **Model** | **Term** | **Estimate** | **SE** | ***df*** | ***t*** | ***P*** | ***R2m*** | ***R2c*** |
|---|---|---|---|---|---|---|---|---|---|
| **Speed** | Initial | Intercept | 4.22 | 5.01 | 220 | 0.84 | 0.401 | | |
| | | Gear (net) | 1.45 | 1.70 | 220 | 0.85 | 0.395 | | |
| | | Temperature (warm) | 0.30 | 0.97 | 220 | 0.31 | 0.756 | | |
| | | TL Average | 0.08 | 1.99 | 220 | 0.04 | 0.968 | | |
| | | TL Variance | 3.20 | 3.59 | 220 | 0.89 | 0.373 | | |
| | | Gear * Temperature | 0.30 | 1.30 | 220 | 0.23 | 0.819 | | |
| | Final | Intercept | 5.08 | 0.45 | 224 | 11.33 | **<0.001** | 0.017 | 0.017 |
| | | Gear (net) | 1.26 | 0.64 | 224 | 1.99 | 0.048 | | |
| **Exploration** | Initial | Intercept | 923.12 | 404.55 | 31.82 | 2.28 | 0.029 | | |
| | | Gear (net) | -245.65 | 137.23 | 31.81 | -1.79 | 0.083 | | |
| | | Temperature (warm) | 84.65 | 78.45 | 31.79 | 1.08 | 0.289 | | |
| | | TL Average | -31.45 | 161.08 | 31.82 | -0.20 | 0.846 | | |
| | | TL Variance | -133.63 | 290.24 | 31.80 | -0.46 | 0.648 | | |
| | | Gear * Temperature | 3.15 | 104.86 | 31.89 | 0.03 | 0.976 | | |
| | Final | Intercept | 822.76 | 42.23 | 34.80 | 19.48 | **<0.001** | 0.241 | 0.604 |
| | | Gear (net) | -210.44 | 49.62 | 34.87 | -4.24 | **<0.001** | | |
| | | Temperature (warm) | 87.06 | 49.69 | 34.88 | 1.75 | 0.089 | | |
| **AND** | Initial | Intercept | -1.23 | 8.23 | 31.84 | -0.15 | 0.882 | | |
| | | Gear (net) | 8.63 | 2.79 | 31.84 | 3.09 | **0.004** | | |
| | | Temperature (warm) | 1.34 | 1.60 | 31.83 | 0.84 | 0.408 | | |
| | | TL Average | 2.49 | 3.28 | 31.84 | 0.76 | 0.454 | | |
| | | TL Variance | 8.52 | 5.91 | 31.83 | 1.44 | 0.159 | | |
| | | Gear * Temperature | -0.29 | 2.13 | 31.89 | -0.13 | 0.894 | | |

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|---|---|---|---|---|---|---|---|---|---|
| | Final | Intercept | 6.91 | 0.74 | 35.81 | 9.27 | **<0.001** | 0.375 | 0.775 |
| | | Gear (net) | 6.00 | 1.05 | 35.88 | 5.69 | **<0.001** | | |
| **Arena Boldness** | Initial | Intercept | 24.02 | 7.09 | 32.02 | 3.39 | **0.002** | | |
| | | Gear (net) | -0.60 | 2.40 | 32.01 | -0.25 | 0.804 | | |
| | | Temperature (warm) | -1.14 | 1.37 | 32.00 | -0.83 | 0.413 | | |
| | | TL Average | -0.29 | 2.82 | 32.02 | -0.10 | 0.918 | | |
| | | TL Variance | -4.46 | 5.09 | 32.01 | -0.88 | 0.387 | | |
| | | Gear * Temperature | -1.08 | 1.84 | 32.08 | -0.59 | 0.561 | | |
| | Final | Intercept | 22.59 | 0.60 | 35.99 | 37.62 | **<0.001** | 0.064 | 0.597 |
| | | Temperature (warm) | -1.75 | 0.87 | 36.08 | -2.00 | 0.053 | | |

**Supplementary Table 5.3)** Model outputs for novel object tests. Mode outputs include results from the initial and final models.

| **Trait** | **Model** | **Term** | **Estimate** | **SE** | ***df*** | ***t*** | ***P*** | ***R2m*** | ***R2c*** |
|---|---|---|---|---|---|---|---|---|---|
| **Speed** | Initial | Intercept | 3.99 | 5.22 | 30.71 | 0.77 | 0.450 | | |
| | | Gear (net) | 2.25 | 1.77 | 30.44 | 1.27 | 0.214 | | |
| | | Temperature (warm) | 0.37 | 1.01 | 30.39 | 0.36 | 0.720 | | |
| | | TL Average | 0.23 | 2.08 | 30.63 | 0.11 | 0.912 | | |
| | | TL Variance | 3.64 | 3.76 | 30.66 | 0.97 | 0.341 | | |
| | | Gear * Temperature | -0.59 | 1.35 | 31.45 | -0.43 | 0.668 | | |
| | Final | Intercept | 5.33 | 0.46 | 225 | 11.68 | **<0.001** | 0.024 | 0.024 |
| | | Gear (net) | 1.51 | 0.64 | 225 | 2.34 | **0.020** | | |
| **Exploration** | Initial | Intercept | 1005.87 | 563.59 | 32.89 | 1.79 | 0.084 | | |
| | | Gear (net) | -267.55 | 191.48 | 32.86 | -1.40 | 0.172 | | |

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|---|---|---|---|---|---|---|---|---|---|
| | | Temperature (warm) | 51.76 | 109.89 | 32.86 | 0.47 | 0.641 | | |
| | | TL Average | -85.51 | 224.34 | 32.88 | -0.38 | 0.706 | | |
| | | TL Variance | 141.51 | 406.79 | 32.88 | 0.35 | 0.730 | | |
| | | Gear * Temperature | 10.04 | 145.29 | 32.95 | 0.07 | 0.945 | | |
| | Final | Intercept | 844.29 | 49.21 | 36.86 | 17.16 | **<0.001** | 0.159 | 0.772 |
| | | Gear (net) | -211.1 | 68.77 | 36.97 | -3.07 | **0.004** | | |
| **AND** | Initial | Intercept | -2.62 | 7.42 | 32.75 | -0.35 | 0.726 | | |
| | | Gear (net) | 4.28 | 2.52 | 32.72 | 1.70 | 0.099 | | |
| | | Temperature (warm) | 0.94 | 1.45 | 32.70 | 0.65 | 0.521 | | |
| | | TL Average | 2.71 | 2.95 | 32.75 | 0.92 | 0.366 | | |
| | | TL Variance | 5.92 | 5.35 | 32.74 | 1.11 | 0.277 | | |
| | | Gear * Temperature | 2.41 | 1.91 | 32.85 | 1.26 | 0.217 | | |
| | Final | Intercept | 4.51 | 0.82 | 35.67 | 5.53 | **<0.001** | 0.209 | 0.717 |
| | | Gear (net) | 3.01 | 0.95 | 35.81 | 3.17 | **0.003** | | |
| | | Temperature (warm) | 1.98 | 0.95 | 35.83 | 2.08 | **0.044** | | |
| **Arena Boldness** | Initial | Intercept | 23.95 | 7.09 | 33.01 | 3.38 | **0.002** | | |
| | | Gear (net) | -1.57 | 2.41 | 32.98 | -0.65 | 0.520 | | |
| | | Temperature (warm) | -1.84 | 1.38 | 32.98 | -1.33 | 0.193 | | |
| | | TL Average | -1.01 | 2.82 | 33.00 | -0.36 | 0.723 | | |
| | | TL Variance | -5.93 | 5.12 | 33.00 | -1.16 | 0.255 | | |
| | | Gear * Temperature | 0.90 | 1.83 | 33.07 | 0.49 | 0.625 | | |
| | Final | Intercept | 20.29 | 0.76 | 35.96 | 26.63 | **<0.001** | 0.047 | 0.749 |
| | | Gear (net) | 0.08 | 0.89 | 36.05 | 0.09 | 0.926 | | |

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|---|---|---|---|---|---|---|---|---|---|
|  |  | Temperature (warm) | -1.39 | 0.89 | 36.06 | -1.57 | 0.126 |  |  |
| **Novel Object Boldness** | Initial | Intercept | 44.98 | 14.56 | 31.99 | 3.09 | **0.004** |  |  |
|  |  | Gear (net) | -11.39 | 4.93 | 31.99 | -2.31 | **0.028** |  |  |
|  |  | Temperature (warm) | -4.27 | 2.81 | 31.99 | -1.52 | 0.139 |  |  |
|  |  | TL Average | -10.01 | 5.80 | 31.99 | -1.73 | 0.094 |  |  |
|  |  | TL Variance | 15.75 | 10.43 | 32.00 | 1.51 | 0.141 |  |  |
|  |  | Gear * Temperature | 4.53 | 3.78 | 32.02 | 1.20 | 0.239 |  |  |
|  | Final | Intercept | 21.03 | 1.33 | 36.00 | 15.77 | **<0.001** | 0.072 | 0.881 |
|  |  | Gear (net) | -3.42 | 1.89 | 36.02 | -1.82 | 0.078 |  |  |