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Investigating the impacts
of environmental change on
social behaviour in fish

Molly Clark

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Masters' by Research in the School of Biological Sciences, Faculty of Life Sciences in September, 2022.

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Abstract

Investigating the impacts of environmental change on social behaviour in fish

Social behaviours occur between individuals across the animal kingdom and mediate a variety of essential fitness related processes. The interactions between individuals can change depending on differences between individuals (e.g. in physiological state or personality) and ecological context. Anthropogenic impacts are rapidly changing the environment through climate change, pollution and habitat fragmentation. Individuals will alter their behaviour as a result of these changes, which can have consequences for social interactions and the maintenance of animal groups. The aims of this research are to investigate the impacts of environmental conditions on social associations in fish shoals. Using two distinct approaches and measuring social interactions at different scales I consider how environmental conditions can alter the dynamics of these groups. Presenting a novel field method, I explore the impact of several environmental conditions on social behaviour in populations of three-spined sticklebacks (*Gasterosteus aculeatus*). Temperature, season, light intensity and dissolved oxygen were found to alter the numbers of fish caught. The only variable affecting aggregation of sticklebacks was their reproductive state, where populations were less aggregated during the breeding season. Under controlled laboratory conditions I investigate how acoustic noise can alter group dynamics in groups of Trinidadian guppies (*Poecilia reticulata*), analysing behaviour with video tracking software. Added noise had no effect on the activity or exploration behaviour of individuals, nor the cohesion of groups. Guppies displayed more following behaviour in the control versus the noise treatment, providing evidence that noise can alter decision-making dynamics in shoals of guppies. Together, these studies provide a broader insight into how social dynamics in fish shoals can change under different environmental contexts and at different scales. This work establishes areas that require more attention in future considerations of how, and the extent to which, environmental change may impact social species at a broader scale.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: Molly Clark DATE: 19th Sept 2021

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Chapter 1

General introduction

Group-living is ubiquitous across the animal kingdom and spans a broad spectrum of complexity and scales. Social groups range from ephemeral collectives to complex societies with traditions, cultures and distinct morphological castes. Animals aggregate for specific reasons when unified by common fitness needs. Whether gregarious or not, almost all organisms will at some time engage in social interactions, congregating for reproduction or engaging in agonistic interactions. Here, I focus on social behaviours that maintain gregariousness in the context of group-living species.

Living in groups: benefits and maintenance

The benefits of group-living in animals include numerous non-exclusive mechanisms. Perhaps the most dominant theory for the development and maintenance of group-living is the anti-predator benefits it provides (Ioannou, 2017). Reduced predation risk in groups can be most simply explained by the ‘dilution effect’, where the risk of being killed by a predation attempt is reduced in proportion to the number of individuals in the group (Foster and Treherne, 1981; Turner and Pitcher, 1986). Groups can also create confusion effects, where large groups of prey present a cognitive challenge for predators and make predation attempts less successful (Krakauer, 1995; Tosh *et al.*, 2006; Ioannou *et al.*, 2008). Further mechanisms include improved predator detection via group vigilance (Treherne and Foster, 1981; Elgar, 1989), reduced probabilities of prey encounters due to populations being less dispersed (Ioannou, 2011a), and collectively mobbing predators (Graw and Manser, 2007). Dwarf mongooses (*Helogale parvula*) have been found to collectively mob predatory snakes using recruitment calls, and success rates are higher when more group members participate (Kern and Radford,

2016). The costs of these behaviours are also shared among group members and may free up time for individuals to perform other fitness tasks. Aggregation of individuals for anti-predator benefits can occur as a result of both short and long term exposure to predators (Hoare *et al.*, 2004; Herbert-Read *et al.*, 2017a).

Group-living can also improve efficiency in gathering resources, such as through foraging (Ranta and Kaitala, 1991) or cooperative hunting (Bshary *et al.*, 2006). School size was found to improve feeding success in shoals of three-spined sticklebacks (*Gasterosteus aculeatus*; Ranta and Kaitala, 1991) and mixed-species groups of coral reef fish can benefit from hunting together, using complimentary strategies (Vail *et al.*, 2013). Increased foraging success is also related to a reduction in vigilance times per individual when foraging in groups (Bednekoff and Lima, 1998). Starlings (*Sturnus vulgaris*) were able to reduce the time devoted to surveillance when in a group while maintaining effective predator vigilance (Powell, 1974). Furthermore, higher sociability can provide individuals a greater opportunity to discover novel food, a result of using social information available to those individuals with more social connections (Aplin *et al.*, 2012). Here, social information provides a benefit to individuals success, where searching in groups allows individuals to maximise their efficiency (Giraldeau, 1984; Lachlan *et al.*, 1998; Krause and Ruxton, 2002).

Individuals can also benefit from shared labour when in a group, where important fitness tasks are divided among the group to improve productivity towards a shared goal (Smith and Riehl, 2022). This is primarily found in societies of eusocial insects (Robinson, 1992), which often display remarkable division of cooperative labour, including of queens and workers, and further subdivisions within worker castes (Reeve *et al.*, 1998; Barker *et al.*, 2016). Workers may divide up tasks based on age, whereas some develop distinct morphologies that allow

only the most specialised individuals to undertake specific tasks, such as colony defence (Grüter *et al.*, 2012). The degree of cooperation will vary with relatedness, as explained by Hamilton's rule which states that for cooperation to occur: the cost of a behaviour must be outweighed by the benefit to the recipient, multiplied by the relatedness (Hamilton, 1964). This explains why individuals can undergo drastic changes, such as loss of reproduction, to maintain social groups and still incur positive fitness benefits overall. However, other systems have found helpers were unrelated, suggesting other factors are also at play (Quiñones *et al.*, 2016; Kingma, 2017). Division of labour is also found in other animal groups (Smith and Riehl, 2022), such as the hierarchical group structures of meerkats, where dominant individuals dominate reproduction and subordinates spend more time caring for pups (Clutton-Brock *et al.*, 2004).

Further, group-living can reduce the energetic costs associated with movement. In fish, schooling can reduce energy expenditure at any position, where tailing is the most efficient (Svendsen *et al.*, 2003; Marras *et al.*, 2015). These benefits are unbalanced among group members due to consistent positional organisation of some members at the less costly tailing end (Svendsen *et al.*, 2003). However, Killen *et al.*, (2012) found that aerobic capacity influenced the position individuals occupy within schools, where individuals can optimise their energy expenditure relative to internal state, thus shoaling reduces the cost of swimming. Further, those individuals with a higher aerobic capacity could occupy more physically challenging positions in the school which allow them to take advantage of higher food availability (Killen *et al.*, 2012). Thus, being in a group can allow individuals to maximise their individual needs and efficiency.

Mechanisms of group-living: social behaviours and information

Group-living is often mediated by social interactions that facilitate the sharing of information between individuals. Access to this social information is one of the major benefits of social behaviour (Danchin *et al.*, 2004; Dall *et al.*, 2005) and is maintained by various mechanisms that range in complexity.

One fundamental aspect of group-living is collective movement. Coordinated movement is required to maintain cohesion and cooperation in groups. In the absence of centralised control individual members must respond to one another based on local interactions, giving rise to coordinated global movement of groups, a mechanism termed self-organisation (Camazine *et al.*, 2001; Sumpter, 2006; Garnier *et al.*, 2007). This self-organisation is mediated by cues and simple interaction rules (Parrish and Edelstein-Keshet, 1999; Ballerini *et al.*, 2008). These interactions, and other social behaviours, are required for individuals to share information with one another and maintain cohesive movement. In some cases, groups collate their information and achieve accurate decisions by averaging all group members estimates. This is known as the “many wrongs” principal (Bergman and Donner, 1964). By averaging all members information the most accurate decision is achieved (Simons, 2004; Codling *et al.*, 2007; Guttal and Couzin, 2010). As a result, larger groups can make more accurate decisions (Surowiecki, 2004) which has been well documented in studies of homing pigeons (Keeton, 1970; Tamm, 1980; Biro *et al.*, 2006). Such decisions may be related to where to move (Trillmich *et al.*, 2004; Couzin *et al.*, 2005), or as a result of choosing between nest sites (Seeley and Buhrman, 1999), activities (Conradt, 1998; Ruckstuhl and Neuhaus, 2000), or hunting strategies (Conradt and Roper, 2005).

In some cases, decisions are shared among group members and can be governed by quorum decision-making, where groups agree on where to move through a shared process (Sumpter and Pratt, 2008). Quorum decisions operate by positive feedback, where the probability that an individual will perform a behaviour is dependent on how many others in the group are performing the same behaviour (Sumpter and Pratt, 2008). Examples of these democratic movement decisions have been shown in ants (Pratt *et al.*, 2002), fish (Ward *et al.*, 2008) and primates (Strandburg-Peshkin *et al.*, 2015). Conversely, group-decisions can be controlled by a minority of the group, and leaders can exert more influence on group activity (Ioannou *et al.*, 2015). Leadership can emerge when some individuals are more informed than other group members (Ioannou *et al.*, 2015; Reeb, 2000) or are more motivated towards a goal, e.g. more urgently require resources (Conradt *et al.*, 2009). In other cases, leaders emerge based on individual differences including boldness (Ward *et al.*, 2004; Harcourt *et al.*, 2009; Webster and Ward, 2011; Jolles *et al.*, 2015) and dominance (Peterson *et al.*, 2002; King *et al.*, 2008; Flack *et al.*, 2013). Hierarchy can have a stronger influence on leadership than experience or knowledge, where more dominant individuals exert more influence on decisions and act as leaders (Peterson *et al.*, 2002; King *et al.*, 2008; Flack *et al.*, 2013).

Individuals may also gain social information from groupings through social learning. This process allows more informed or experienced group members to influence decisions more, or guide naïve members who in turn learn the information for themselves (Galef and Laland, 2005; Hoppitt and Laland, 2013). This often occurs through naïve individuals copying the behaviour of those they are learning from (Galef and Laland, 2005). In bird migrations, social learning can benefit the accuracy of groups (Mueller *et al.*, 2013; Aikens *et al.*, 2022). Animals use different mechanisms to share information with group members. Honeybees waggle dances provide group members with information about the quality of resources and where to find them,

allowing the colony to collectively move towards the unexploited resource (Judd, 1994; Franks *et al.*, 2002). Social learning can also result in behaviours being transmitted through a population, developing into learned traditions (Galef 1988) such as novel foraging behaviour (Lefebvre and Palameta, 1988). This can also develop into culture in animal societies, such as tool-use in primates, where cultural traditions vary across populations resulting in regional variation (Matsuzawa *et al.*, 2001; Biro *et al.*, 2003).

Costs of group-living: conflict and poor decisions

Despite the benefits provided by group-living it is not without cost (Grand and Dill, 1999; Krause and Ruxton, 2002). Being in a group can have detrimental fitness effects, such as increased conspicuousness when individuals are aggregated leading to increased predation attempts (Krause and Ruxton, 2002). Grouping can also facilitate higher rates of disease transmission, and increased competition for resources such as food or mates (Krause and Ruxton, 2002).

Furthermore, the mechanisms by which collective behaviour and social interactions are mediated are not without fault and can involve conflicts. Ultimately, individuals often make decisions based on maximising their own fitness, which may sometimes be detrimental to group cohesion. When the cost of compromising on a decision is higher than the benefits provided by groupings, groups should disperse (Smith *et al.*, 2016). The degree to which there are conflicts of interest in decisions varies (Conradt and Roper, 2005; 2009). In some cases, individuals all have a shared goal, thus conflicts within the group are low, for example in migrating or homing bird flocks (Biro *et al.*, 2006; Simons, 2004). In other cases, individuals may have different internal states that mean they have different requirements, and decisions

involve substantial conflict (Gompper, 1996; Conradt and Roper, 2009). This disparity in motivation can result in certain individuals gaining disproportionate weight in decision outcomes (Krause, 1993; Conradt and Roper, 2009). This may be exacerbated in situations involving leadership, where a behaviour is beneficial to the leader since it is acting on its own interests, but may not be the optimal choice for the rest of the group (Conradt and Roper, 2003; 2009). Here, the benefits of a behaviour are asymmetrical across group members, and can actually lead to a reduction in the fitness of individuals within the group. Dominance hierarchies in groups can exacerbate these problems, where followers can be coerced into making suboptimal decisions for their own fitness, or where the dominant leaders are not those with the most experience or information (Peterson *et al.*, 2002; King *et al.*, 2008; Flack *et al.*, 2013).

Ecological variation: social behaviour depends on environmental context

In the same way individual motivations and states alter behaviour, environmental conditions can have impacts on the way individuals behave and interact with one another. After all, ecological conditions are what initially lead to the evolution of adaptive behaviour. The costs and benefits of being in a group are not constant, but fluctuate as a result of these individual differences and changes in the environment. Such changes mean that grouping is beneficial in one scenario but not another. Whether or not gregariousness is favoured depends on the fitness requirements of individuals which change in different contexts (Herbert-Read *et al.*, 2011).

Temperature changes can alter the energetic state of individuals. Thermal stress can reduce the energy individuals have available, and in turn reduce their ability to perform social behaviours (Fisher *et al.*, 2021). Conversely, warmer conditions can reduce energetic constraints and result

in increased communication between individuals, for example as found in ovenbirds (*Seiurus aurocapilla*) who sing more on warmer days (Foote *et al.*, 2017). In aquatic environments higher temperatures reduce the oxygen holding capacity of water, resulting in hypoxia. Hypoxia can reduce social interactions due to individuals prioritising oxygen access over shoaling (Moss and McFarland, 1970; Israeli and Kimmel, 1996; Domenici *et al.*, 2002). Higher temperatures can also affect the stability of social structures like dominance hierarchies. In experimental trials using Amazonian dwarf cichlids (*Apistogramma agassizii*) warmer water and hypoxia altered aggression levels and disrupted social hierarchy (Kochhann *et al.*, 2015).

Some environmental conditions alter the medium in which signals and cues are transmitted and received, and such changes can alter individual's ability to perceive information from the environment and their group-mates (Fisher *et al.*, 2021). Light is an essential part of the environment for visual signals. Increases in light intensity results in more conspicuous signals, and in turn leads individuals to perform higher rates of signalling (Kurvers and Hölker, 2015). Underwater, light intensity can change based on turbidity levels, which has been shown to restrict visual communication in a range of fish taxa including three-spined sticklebacks (*Gasterosteus aculeatus*; Candolin *et al.*, 2007), pipefish (*Syngnathus typhle*; Sundin *et al.*, 2010), and sand gobies (*Pomatoschistus minutus*; Järvenpää and Lindström, 2004). The impacts of environmental conditions on social behaviours and interactions can result in further changes to social structures, grouping associations and collective behaviour (Fisher *et al.*, 2021).

Anthropogenic disturbance: consequences for social behaviour

Human impacts on the environment are leading to rapid and unprecedented changes to environmental conditions far beyond what is expected in naturally occurring fluctuations. Global climate change, added pollutants, and habitat fragmentation all alter environmental conditions. These effects can induce changes in temperature, and increase the prevalence of artificial light, noise and chemicals, among many other stressors (Fisher *et al.*, 2021). It is also important to consider that these stressors are not occurring in isolation but are in fact happening simultaneously (termed 'multiple stressors'; Wong and Candolin, 2015; Orr *et al.*, 2020). Multiple aspects of the environment can be influencing the behaviour of individuals, and can result in additive, antagonistic or synergistic effects (Orr *et al.*, 2020; Ginnaw *et al.*, 2020).

When animals attempt to modify their behaviour to the novel conditions brought about by anthropogenic change, or are put under increased stress by them, social interactions are likely to be altered as well (Fisher *et al.*, 2021). This can have knock on effects for social groupings, causing them to become more or less aggregated. Disruption of social groupings, a result of environmental context altering individuals needs and the benefits they gain from sociability, could cause them to disperse and lose all benefits provided by gregariousness (Fisher *et al.*, 2021).

Behavioural changes in response to environmental stressors can be short-term beneficial modifications and may have no impact on the cohesion and productivity of groups. Alternatively, these changes could produce more substantial or long-term effects, with unknown and potentially disadvantageous consequences (Da Silva *et al.*, 2016). This can alter how individuals interact with one another. Given the importance of social interactions and

group-living for many species, understanding how these rapid changes in the environment can affect sociability is essential in allowing us to understand its consequences for wider ecosystems, communities, and biodiversity as a whole.

Aims of this research: investigating social behaviour under environmental change

In the research presented in this thesis I examine the degree to which environmental conditions alter social behaviours in two species of freshwater fish. The second chapter comprises a field study designed to investigate social behaviour in a natural context. Here, I highlight the importance and challenges of understanding the role ecological context plays in the behaviours of social species. The third chapter comprises a laboratory study, focusing on acoustic noise as a pollutant. Within a controlled laboratory environment, I was able to use tracking software to assess behaviour, including decision-making, at the individual and group-level. Social behaviour occurs at both broad and fine scales, from the aggregation patterns of whole populations to local inter-individual interactions. In these two studies I examine changes relating to ecological conditions at these two distinct levels. In the final chapter I discuss the broader implications of these two studies and what they have highlighted about future directions for research.

Chapter 2

A novel method for investigating fish social behaviour in the field

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Abstract

Field studies of social behaviour are challenging due to having to observe multiple individuals simultaneously. In aquatic environments, these challenges are often amplified by environmental conditions such as habitat complexity, turbidity or darkness, which are often conditions of interest in the context of studying anthropogenic impacts. Many fish species rely on social interactions for at least part of their life cycle, and while these interactions are known from laboratory studies to be impacted by environmental factors, approaches to quantify social behaviour under natural conditions are limited. Here, we present a novel method whereby multiple funnel traps are deployed simultaneously within a pond to quantify the aggregation and assortment of wild fish populations, using three-spined sticklebacks (*Gasterosteus aculeatus*) as a model species. The number of sticklebacks caught decreased as temperatures fell, and through the seasons, from May to November. There was some evidence for decreases in fish numbers with reduced light intensity and higher dissolved oxygen levels. No effect of turbidity was found. The only evidence for changes in aggregation was related to the proportion of breeding males caught, where sticklebacks were less aggregated during the breeding season. These trends are expected based on previous work and knowledge about stickleback biology, validating the method. However, in contrast to previous studies, we found little evidence for assortative grouping by body size. This study establishes a new cost-effective technique for investigating the social behaviour of wild fish, with some important benefits over existing techniques.

Introduction

Social behaviour is essential for the reproduction and survival of many fish species, in at least part of their life cycle. Being in a group provides hydrodynamic (Svendsen *et al.*, 2003; Killen *et al.*, 2012; Marras *et al.*, 2015), reproductive (Taborsky, 2001), foraging (Ranta and Kaitala, 1991) and anti-predator benefits (Ioannou, 2021), as well as costs (Grand and Dill, 1999; Krause and Ruxton, 2002). These benefits and costs associated with shoaling can change depending on environmental conditions, altering group dynamics through adaptive changes in individuals' behaviour (Pitcher and Parrish, 1993). Environmental conditions can also interfere with and constrain the inter-individual interactions that allows for group formation and maintenance (Chamberlain and Ioannou, 2019; Ginnaw *et al.*, 2020). Because of widespread environmental change due to human activity, it is increasingly important to study the effect of environmental factors on social behaviour so we can understand changing dynamics in wild populations, especially in freshwater environments (Ormerod *et al.*, 2010).

Current methods for studying fish social behaviour in the field mostly depend on cameras, or use of seine nets to capture whole shoals (Sarà *et al.*, 2007; Croft *et al.*, 2009; Burford *et al.*, 2022). These methods are often restricted by environmental conditions, particularly those which reduce water clarity, such as turbidity and darkness, making shoals harder to visually find and identify for netting or recording. Higher light intensity can also produce problems for image and video quality as a result of 'sunflicker', increasing visual noise (Gracias *et al.*, 2009), and more complex habitats with dense vegetation can add barriers to visibility and create more general access problems. These factors also reduce the ability to analyse videos through tracking software, which generally require a high resolution and contrast between subject and background (Dell *et al.*, 2014). Techniques that overcome some of these environmental limitations are often expensive and come with their own constraints. Thermal or sonar imaging

allow recording in the field when there is poor water clarity, however have limited spatial and temporal resolutions (Hughey *et al.*, 2018; Rodriguez-Pinto *et al.*, 2020). Additionally, these technologies present challenges for the identification of species, where it is hard to decipher the species being imaged. Alternatively, tracking technologies such as GPS or PIT tags overcome the problems of view, access, and spatial constraints, but require every individual fish to be caught and tagged (Hughey *et al.*, 2018). Measuring group behaviour ideally requires data to be collected from a large proportion of the population to avoid missing social interactions, thus these methods involve extensive handling and equipment to reach this goal. These tags can also be invasive with implication for welfare, and it is unclear to what extent they affect the natural behaviours of tagged individuals.

Freshwater ecosystems face multiple threats from environmental change, such as eutrophication and increasing temperatures, and the combined effects of these and other stressors such as overfishing (Carpenter *et al.*, 2011; Angeler *et al.*, 2014; Orr *et al.*, 2020). Driven by anthropogenic change, such as urbanisation and agriculture, increased runoff of sediments and pollutants can generate eutrophication and turbidity levels in water that far exceed natural fluctuations (Davies-Colley and Smith, 2001). Elevated turbidity restricts the visual environment for aquatic animals and visibility often deteriorates rapidly, preventing species from being able to adapt to the new conditions (Davies-Colley and Smith, 2001; Chamberlain and Ioannou, 2019). Deforestation can also reduce habitat complexity, leading to fewer foraging opportunities and refuges, and can result in less diverse fish assemblages (Bojsen and Barriga, 2002; Zeni *et al.*, 2019). The subsequent reductions in canopy cover from deforestation can also lead to increases in light intensity over streams, creating more noise in the visual environment, e.g. from caustics (where the refraction and reflection of light creates visual patterns on the water surface), and contribute to warmer temperatures (Ilha *et al.*, 2018;

Matchette *et al.*, 2018; 2020). With continued pressure on freshwater environments it is increasingly important to understand how these and other stressors are affecting fish communities and their social behaviour. However, restrictions from environmental conditions on field techniques are often the same environmental conditions that we want to study, such as water turbidity, and novel methods are required to explore their impact on fish social behaviour.

Empirical studies have demonstrated that changes in environmental conditions can impact social interactions in fish. Through masking, environmental stressors can disrupt information transfer between individuals, and thus their ability to maintain coordinated shoals (McNett *et al.*, 2010). For example, turbidity and low light intensity restricts the use of visual information among shoal members, leading to reduced group cohesion, coordination, and collective decision-making (Pitcher and Turner, 1986; Ryer and Olla, 1998; Ohata *et al.*, 2014; Chamberlain and Ioannou, 2019; Ginnaw *et al.*, 2020). Consequently, individuals reduce their foraging efficiency and lose the anti-predator benefits provided by shoaling (Chamberlain and Ioannou, 2019). Stressors can also shift focus away from group behaviour via distraction (Chan *et al.*, 2010). For example, although there is limited evidence that acoustic cues or signals are used in fish shoaling (Ioannou *et al.*, 2011b), anthropogenic noise pollution has been shown to shift the attention of individuals, and in turn reduce the coordination and cohesion of shoals (Sarà *et al.*, 2007; Voellmy *et al.*, 2014a; Herbert-Read *et al.*, 2017b).

A reduced ability to perceive potential threats can also result in direct stress (Pitcher and Turner, 1986; Sutherland *et al.*, 2008; Ohata *et al.*, 2014). Stress occurs when individuals are unable to maintain normal physiological functions due to higher demands on the body from the environment (Schulte, 2014), in contrast to masking and distraction which affect behaviour and the efficacy of sensory system perception. Stress can be caused by temperature changes

which alter the energetic states of fish, affecting activity and limiting the energy individuals have available or altering internal states so individuals in a group differ (Fisher *et al.*, 2021). Stress can be measured by cortisol levels (Wysocki *et al.*, 2006; Sadoul and Geffroy, 2019). Temperature changes can therefore affect the hydrodynamic benefits of shoaling, where higher temperatures result in less cohesive groups (Weetman *et al.*, 1998; Bartolini *et al.*, 2015). The impact of temperature is often confounded with oxygen concentrations, where in hypoxic conditions reduced shoaling is caused by a trade-off between maintaining close, cohesive shoals and accessing oxygen (Moss and McFarland, 1970; Israeli and Kimmel, 1996; Domenici *et al.*, 2002). Hypoxia can also be a result of eutrophication (Rydberg *et al.*, 1990; Hagy *et al.*, 2004), and similar impacts can be found as a response to chemical pollutants, where chemicals interfere with physiology and can reduce social interactions (Webber and Haines, 2003; Brodin *et al.*, 2013; Michelangeli *et al.*, 2022). The masking, distraction, and stress effects caused by environmental change rarely occur in isolation, they can influence social behaviour in different and combined ways, and field studies can help elucidate the impacts of such change on natural freshwater populations and environments.

Taking the restrictions of current techniques into consideration, and the threats faced by freshwater fish communities, we have developed a method using passive funnel traps (also commonly known as minnow traps) allowing us to compare fish social behaviour in relation to environmental parameters. Here, we can quantify the aggregation and activity of fish populations based on the numbers of fish caught in each trap when deploying five traps simultaneously within a pond. While funnel traps and catch per unit effort have often been used to quantify fish and species abundance in fisheries, and ecological research more broadly, the novelty of our method comes from the simultaneous deployment of the five traps. This design allows us to gain a broader view of aggregation across the whole population in a given time

frame because the number of fish captured in each trap is considered relative to the number of fish captured in every other trap. Due to potential metabolic limitations we would expect to catch fewer fish at lower temperatures, where in colder water fish are less active, but that fish would also be more aggregated (i.e. less distributed across traps) a result of enhancing the energetic benefits of shoaling and reducing their swimming cost in colder temperatures (Bartolini *et al.*, 2015). We also expect fish to be less aggregated in low oxygen conditions, where individuals should seek to maximise their oxygen intake (Domenici *et al.*, 2002). Visual constraints could also lead to fish being less aggregated when turbidity is higher (Ohata *et al.*, 2014; Chamberlain and Ioannou, 2019) and where there is lower light intensity (Pitcher and Turner, 1986), due to vision being an important sensory modality for shoal cohesion (Ioannou *et al.*, 2011b).

Additionally, we measured the body lengths of each caught fish with the aim to quantify the phenotypic assortment of groups. Assortment occurs when there is non-random grouping of individuals that share similar characteristics, including size, and experimental studies have demonstrated a preference for fish to choose to group with those similar to them (Krause *et al.*, 1996; Peuhkuri, 1997; Ranta and Lindström, 1990; Ward and Krause, 2001). Assorting preferentially with individuals that share similar phenotypic traits is potentially adaptive through reduced foraging competition (Peuhkuri, 1997) and improved predator avoidance through predator confusion (Ioannou *et al.*, 2008; Krakauer, 1995).

We used three-spined sticklebacks (*Gasterosteus aculeatus*) as a model species due to their prevalent use in behavioural and genetic research, and because they are commonly found in fresh and brackish water in the UK. Sticklebacks are facultatively social and have been found to prefer to join groups of individuals similar to them in size (Ranta and Lindström, 1990).

They use visual cues in their social behaviours (Huntingford and Ruiz-Gomez, 2009) and previous research has shown this can be affected by environmental conditions such as light and turbidity (Candolin *et al.*, 2007; 2016).

Materials and Methods

Study sites

The study was carried out in four ponds in Bristol, UK (Table 1; Figure 1). Sites were chosen based on having populations of three-spined sticklebacks (*Gasterosteus aculeatus*) of sufficient density to allow enough fish to be caught per site visit for analysis of aggregation and assortment by body size. Site choice was also dependant on accessibility and appropriate water depth for traps to be deployed. Sampling carried out at these sites was approved by the Environment Agency UK.

Table 1. Mean \pm standard deviation of environmental variables recorded and numbers of fish caught per site visit and per trap for each of our four sites. These were calculated from the averages (mean) of each variable calculated per site visit. Data was recorded from May to November 2021.

Parameters	Brandon	Pennywell	Sneed	Tarn
National Grid Reference	ST57967293	ST55737783	ST55477549	ST55887818
Temperature (°C)	16.29 \pm 4.40	13.44 \pm 2.75	16.50 \pm 4.03	14.68 \pm 3.80
Turbidity (NTU)	2.72 \pm 1.48	13.09 \pm 8.17	5.25 \pm 1.88	36.43 \pm 14.41
Dissolved O ² (mg/L)	11.35 \pm 1.95	9.21 \pm 1.19	8.63 \pm 2.25	9.06 \pm 1.77
Light (lum/ft ²)	631.49 \pm 445.64	191.15 \pm 171.65	790.83 \pm 644.35	476.83 \pm 265.34
Mean \pm SD catch per site	85.38 \pm 69.66	101.62 \pm 77.25	117.38 \pm 108.77	66.23 \pm 52.63
Mean \pm SD catch per trap	14.68 \pm 19.67	21.92 \pm 33.11	20.72 \pm 30.29	17.26 \pm 28.91

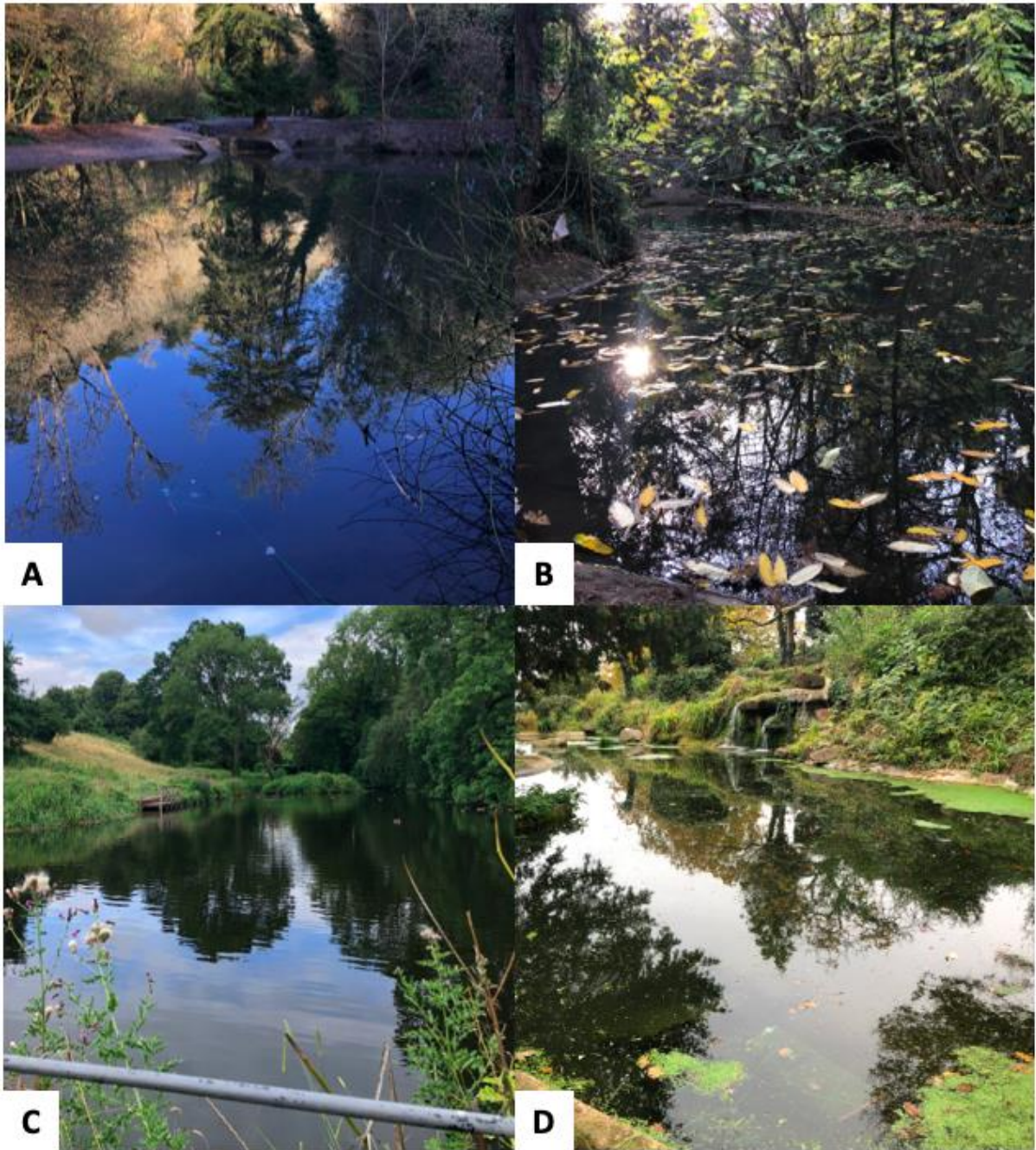


Figure 1. The study sites: (A) Tarn Lake in Blaise Castle (Tarn), (B) Penny Well in Blaise Castle (Pennywell), (C) Old Sneed Park Nature Reserve (Sneed), (D) Brandon Hill Nature Reserve (Brandon).

Experimental Procedure

The study was designed to quantify the aggregation of fish populations by comparing the numbers of fish caught across five funnel traps simultaneously deployed at each visit to a site (Figure 2). Traps were deployed at equidistant locations along a pond, as much as access and water depth allowed (Figure 3); these trap locations were maintained throughout data collection and labelled 1 – 5 from left to right (see pins on Figure 3). Traps were either dropped slowly into the water using the long string attached to the trap (Figure 2) where it was possible to get close enough to the trap location, or thrown by holding two corners of the trap when the trap needed to reach a further distance, for instances where water was too shallow near the bank or there was poor access to the edge of the water. Deployment required careful positioning to ensure the temperature and light intensity logger (HOBO MX2202) attached to each trap was facing upwards in the water, and misalignment would require pulling the trap back in with the string and redeploying in the same location. Traps were not baited to avoid attracting unwanted species; traps were baited in the first week with bread, but tended to attract other species such as carp. After the two-hour sampling period where traps were left in the water undisturbed, they were pulled in using the string attached to each trap. If the trap contained fish it was quickly moved to an area of shallow water in the pond so that all caught fish were fully submerged in pond water but shallow enough to prevent escape through the openings in the trap, allowing time for counting and measuring the fish while preventing unnecessary stress.

Sampling took place on alternating weeks between May and November 2021. Which site was visited on which day during a week of data collection was decided by random shuffling of the sites in R version 3.3.3 (R Core Team, 2017). Traps were left for two hours between either 10am – 12pm (AM) or 1pm – 3pm (PM) to account for any confounding effect of time of day.

The first sampling time for each site was chosen by coin-flip, and alternated between AM and PM thereafter.

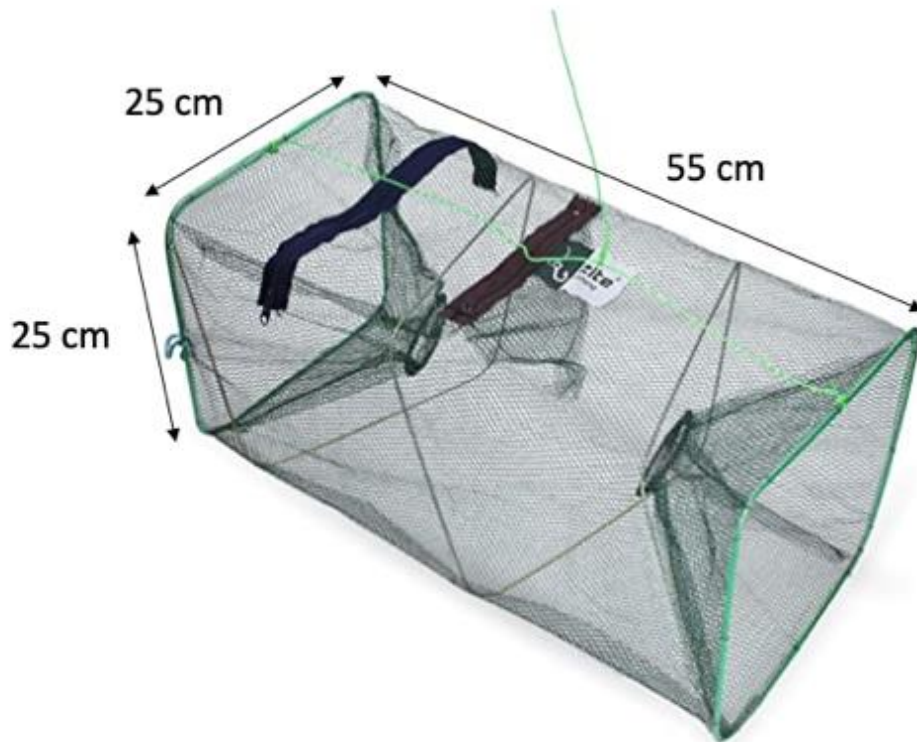


Figure 2. Zite fishing bait fish trap with 5mm small mesh and 2mm thick wire frame.

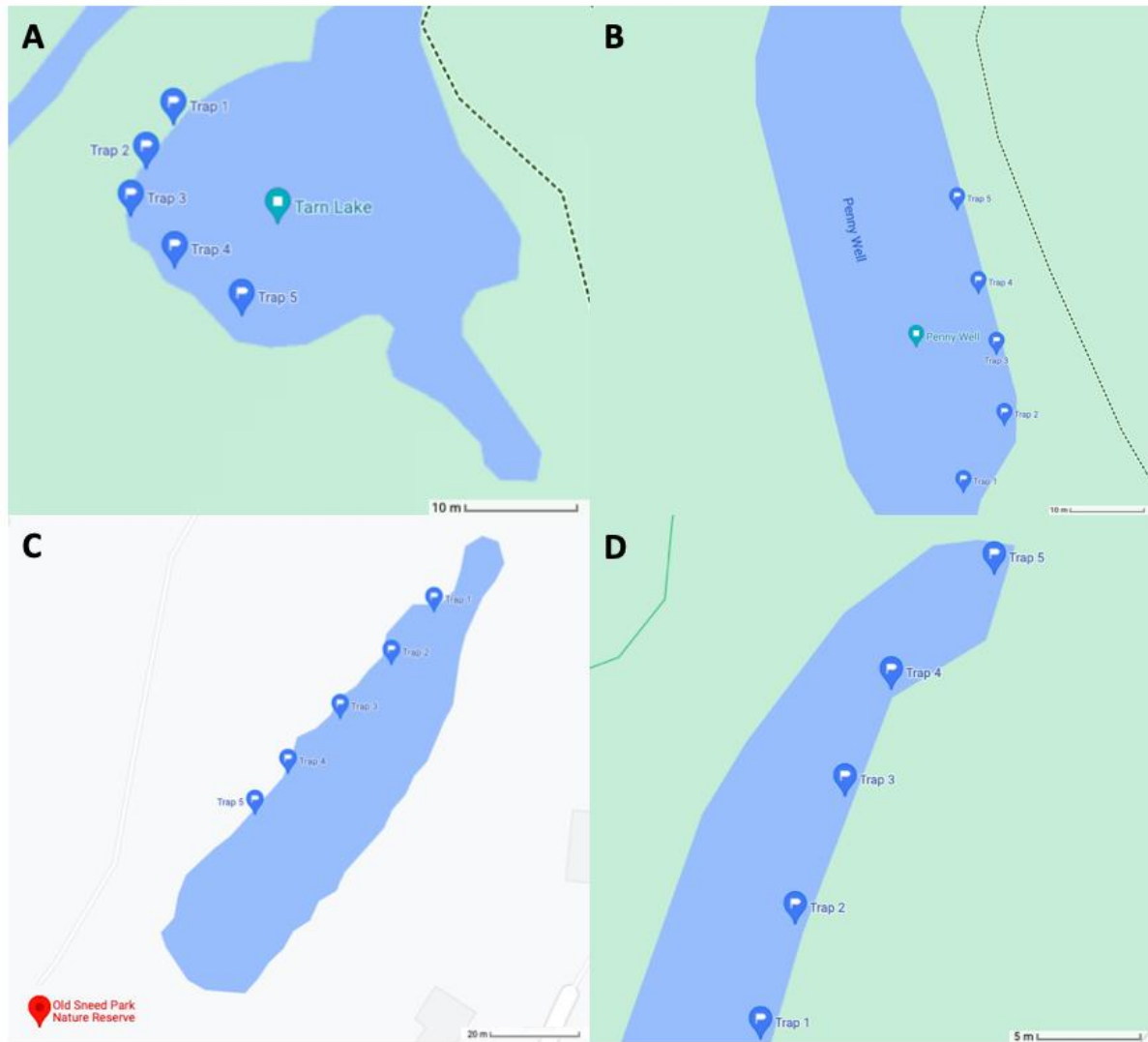


Figure 3. Map of each field site. Blue pins indicate trap locations from 1 – 5. A. Tarn: mean distance between traps 4.7 m, total size ~0.075 hectares; B. Pennywell: mean distance between traps 6.7 m, total size ~0.16 hectares; C. Sneed: mean distance between traps 8.8 m, total size ~0.25 hectares; D. Brandon: mean distance between traps 4.9 m, total size ~0.016 hectares. Images taken from Google Maps, total size estimated from measurements taken in ImageJ.

Environmental Variables

Water temperature and light intensity were recorded using a HOBO MX2202 attached to each trap, which logged data every minute for the two-hour sampling period. Turbidity and dissolved oxygen were measured from water samples taken at each trap location, with samples taken before and after the traps were deployed (i.e. at the start and end of each site visit). Turbidity was measured using a Thermo Scientific Orion AQUAfast AQ3010 Turbidity Meter, and dissolved oxygen using a Lutron Dissolved Oxygen Meter PDO-519.

Measuring Fish

Fish caught in each trap were counted, also noting the number of males in breeding condition with characteristic red colouration (Huntingford and Ruiz-Gomez, 2009). Body length measurements were taken by placing groups of fish in a bucket (Figure 4) with a 10cm scale bar and water from the pond to a depth of 5 cm. The number of fish in the bucket varied between 1 and 21, depending on the number of fish caught in the traps and their size (a greater number of juveniles could be imaged accurately). A GoPro Hero5 was attached to the side of the bucket, 27 cm above the water surface and oriented downward to give an overhead view of the fish. 4000 x 3000 pixel resolution images were taken in burst mode, where 10 photos were taken over two seconds, repeated multiple times if fish were closely aggregated, with the aim to capture an image where all fish are clearly visible and not overlapping. Body length measurements were then made using ImageJ (version 1.53; Schneider *et al.*, 2012). This allowed for reduced stress to the fish and more efficient data collection than manual handling and measuring each fish individually, for example using callipers.

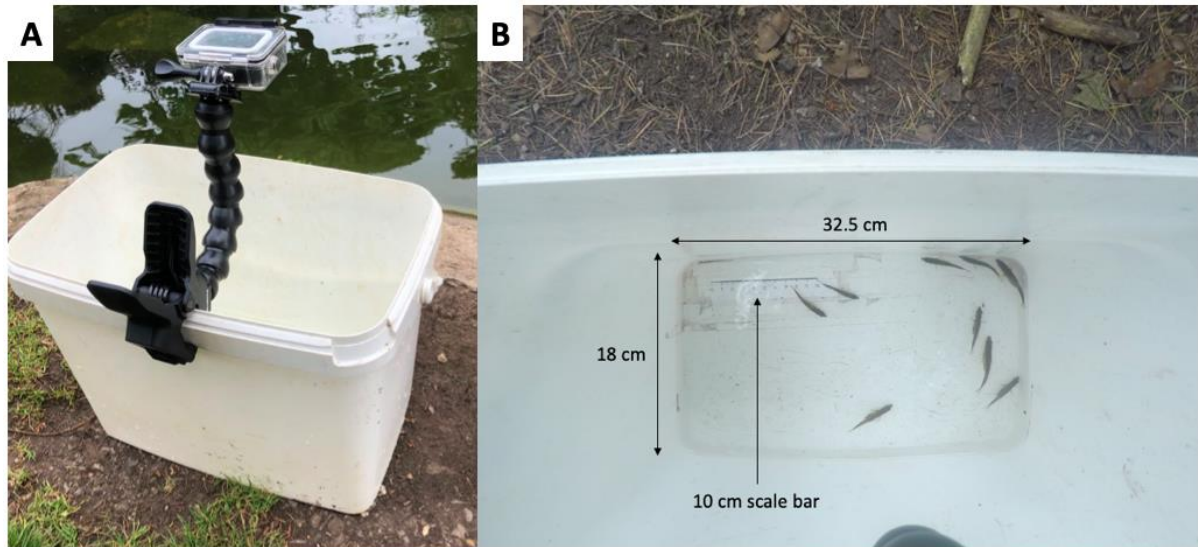


Figure 4. (A) Picture of bucket and camera set up; (B) example of picture with fish in bucket, subsequently used to measure body length in ImageJ (version 1.53).

Statistical analysis

All analyses were conducted in R (version 4.1.2; R Core Team, 2017) using RStudio (version 2021.9.1.375; RStudio Team, 2020). The mean of the temperatures and light intensities recorded from the start to the end of the sampling period at each trap location at one-minute intervals was calculated to give an average temperature and light intensity value for each trap location within each site for every site visit. Turbidity and dissolved oxygen measurements from the start and end of each site visit, from each trap location, were also averaged (mean). When analysing response variables which only had a single value per site visit, rather than at each trap location, for example the total number of fish caught in that visit, these variables were then averaged (mean) across the five trap locations. To test for correlations between the continuous explanatory variables (temperature, light intensity, dissolved oxygen, turbidity, and week of data collection), for both per-trap location and per-site visit values separately, relationships were tested with Spearman's rank correlation coefficient (Spearman's r_s) in R.

To determine which variables could explain the variation in the total number of fish caught at each site visit, we compared 7 generalised linear mixed-effects models (GLMMs) with a negative binomial distribution and default log link function. The response variable was the total number of fish caught per visit to a site, i.e. the sum of the number of fish caught per trap, and the pond site was included as the random effect. Each of the 7 models had a different fixed effect: temperature, light intensity, dissolved oxygen concentration, turbidity, the week of data collection (1 to 13), and whether sampling occurred in the morning or afternoon (AM or PM); a null model with no fixed effect, only the response variable and random effect, was also included in the model comparison set. We then compared the Akaike information criterion values corrected for small samples sizes (AICc) for each model using the `ICtab` function in R (bbmle version 1.0.24; Bolker *et al.*, 2022). Models with lower AICc values are a better fit given the data, and the model with an ΔAICc of zero is the model with the best fit. Explanatory variables included in models that had AICc values of greater than two units less than the null model were considered to be important predictors of the response variable, i.e. these models were considered to have strong support (Burnham and Anderson, 2002). In addition to comparison to the null model, we could also determine which explanatory variables were more likely to predict the variation in the response variable than others.

To explore these trends further, we repeated this process for the number of fish caught per trap, rather than per site visit, as a function of the same explanatory variables with the addition of trap location nested within pond site as the random effect. This allowed us to consider the environmental variation at a smaller spatial scale, at the level of the trap location.

The aggregation of fish between the traps was determined by calculating the index of dispersion (i.e. the variance \div mean) from the number of fish caught in each trap per site visit. An

aggregation score of 0 indicates fish are evenly distributed across the traps, and therefore are not highly aggregated. An aggregation score of 1 indicates fish are randomly distributed across the traps, and higher values indicate fish are more aggregated in a given area (Figure 5A). Cases were removed from the analysis when the total number of fish caught in that visit was too low to show aggregation by this measure (a threshold of 26 fish was determined from plotting the aggregation score as a function of the total number of fish caught; Figure 5A). To determine which variables were likely to predict the aggregation of fish, we compared 8 negative binomial GLMMs. The response variable was the aggregation score for each site visit, and each model had a different explanatory variable: temperature, light intensity, dissolved oxygen concentration, turbidity, week of data collection and morning or afternoon. Here, an additional model was considered, which had the proportion of red-bellied breeding condition males caught (i.e. number of red males \div total fish caught) as an explanatory variable. The eighth model was the null model that lacked an explanatory variable. Pond site was included as the random effect in all models. AICc values were then compared in the same way as previously described.

All GLMMs were run using the `glmmTMB` function (`glmmTMB`; Brooks *et al.*, 2017). The assumptions of all models were verified using QQ plots and dispersion tests using the residual diagnostics for mixed regression models (DHARMA; Hartig, 2019).

As a measure of phenotypic assortment, we used the coefficient of variation (COV; i.e. standard deviation \div mean) of body length, calculated for the fish caught in each trap, excluding cases where only one or no fish were caught in the trap (Figure 5B; Croft *et al.*, 2009). A COV of zero would indicate there is no variation in size between the fish in a trap; the higher a COV value, the more variation (relative to the mean body size) there is in body size between fish in

a trap. The median COV of all the traps at one site visit was used as the observed COV for each site visit (observed siteCOV). To determine whether fish caught in the traps were more or less phenotypically assorted by body length than expected by chance, we calculated the expected median COV for each site visit, assuming random assortment within a visit to a site. The expected value for assortment was calculated using a constrained randomisation procedure in which individuals caught across traps on one site visit were randomly re-distributed across the five traps, maintaining the number of fish caught per trap as in the observed data. The COV of body length was calculated per trap from each resampling, and the median of these values were saved as the value of expected assortment (expected siteCOV). This was iterated 10,000 times for each site visit and an expected distribution of assortment values was generated. The observed siteCOV was used as a quantile on the corresponding expected distribution. In the two-tailed tests, quantiles are statistically significant when < 0.025 , indicating positive assortment (i.e. fish are assorting with those that are similar to themselves), or when > 0.975 , indicating negative assortment (i.e. fish are assorting to those that are different to themselves).

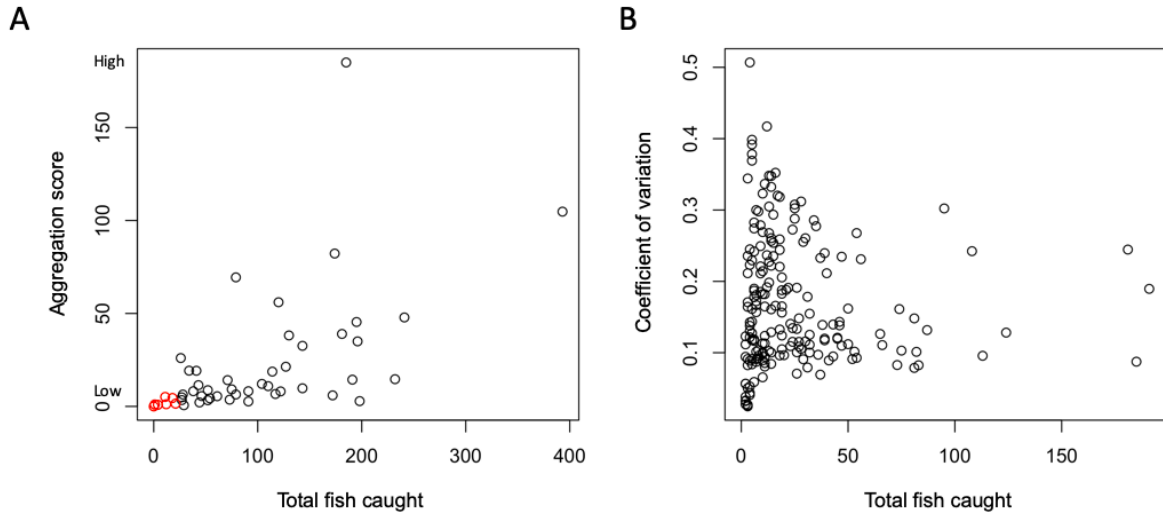


Figure 5. (A) Aggregation scores (index of dispersion, variance \div mean) for each site visit as a function of the total number of fish caught at that site visit. Larger values on the y axis represent cases where fish are more aggregated. Red points indicate data that were removed from the analysis when the total number of fish caught was <26 , where low numbers of caught fish did not produce a representative aggregation score. (B) Coefficient of variation (COV) values for each trap compared to the number of fish caught in that trap. Larger values on the y axis indicate high variation in body length among fish in a trap.

Results

Correlation between explanatory variables

Correlations between the continuous explanatory variables included in the models showed evidence of correlation between temperature and light intensity (Figure 6A; Spearman's rank correlation coefficient: $r_s = 0.60$, $p < 0.0001$, $n = 52$), week and light intensity ($r_s = -0.60$, $p < 0.0001$, $n = 52$), and week and temperature ($r_s = -0.58$, $p < 0.0001$, $n = 52$). Correlation coefficients were similar when using the values measured at each trap location per visit (Figure 6B).

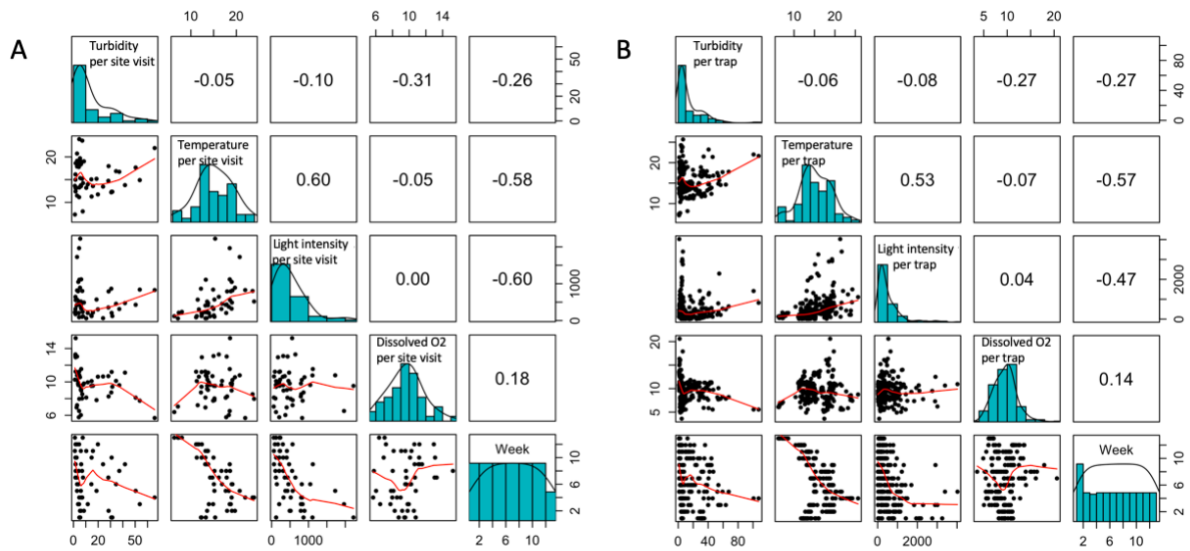


Figure 6. Distributions of, and correlations between, the 5 continuous variables used as explanatory variables in the models. Correlation coefficients are Spearman's r_s . The red curve in the scatter plots are LOWESS smoothed curves. In (A), data is averaged across trap locations giving a value for each site visit. In (B), data includes values of each variable for each trap location per site visit, thus considers within-site variation.

Total fish caught per site visit

Analysis of the total number of fish caught at each site visit showed that the model with week as the explanatory variable was the best fit given the data (Table 2). The total number of fish caught decreased over consecutive weeks of data collection (Figure 7A). The model with temperature as the explanatory variable was less well supported, but being greater than 2 AICc units less than the null model still provides strong evidence that temperature was having an effect on the number of fish caught (Table 2). In this case, the number of fish caught increased in warmer temperatures (Figure 7B). There was some support for the model with light intensity as the explanatory variable, which was 1.1 AICc units less than the null model. Conversely, models where the only explanatory variable was dissolved oxygen, turbidity or the time of day were not supported, indicating that the number of fish caught on a site visit was not associated with variation in these parameters.

Table 2. The $\Delta AICc$ for models explaining variation in the total number of fish caught per site visit. Models differ in the explanatory variable included, and all include pond site as the random effect. The null model has no explanatory variable, only the random effect. Week (week 1-13) and morning or afternoon (sampling in AM or PM) represent when data collection occurred.

Explanatory variable	$\Delta AICc$	d.f
Week	0	4
Temperature	7.5	4
Light intensity	9.4	4
Null model (no explanatory variables)	10.5	3
Dissolved oxygen	11.2	4
Morning or afternoon	11.4	4
Turbidity	12.6	4

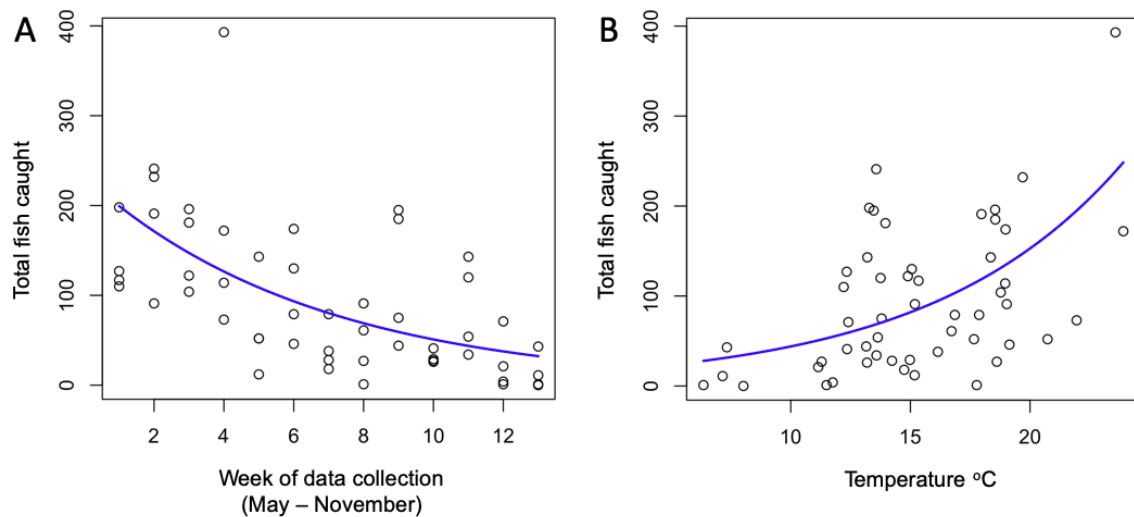


Figure 7. The number of fish caught per site visit as a function of (A) the week of data collection and (B) the average water temperature across the trap locations. Plotted lines show the fitted relationships from GLMM coefficients.

Total fish caught per trap

Analysis of the total number of fish caught per trap, which takes into account environmental variation at each trap location, revealed similar trends to when only averages across a site on a

visit were considered. Week was again the model with the best fit given the data (Table 3), where the number of fish caught decreased over consecutive weeks of data collection from May to November (Figure 8A). The model with temperature was also supported by the data, with the trend again showing the number of fish caught increased with warmer temperatures (Figure 8B). Based on the AICc being higher than the null model, there was no evidence for turbidity or time of data collection having an effect on the number of fish caught at a trap location.

In contrast to the analysis based on the averages from each site visit, the model with dissolved oxygen as the explanatory variable was strongly supported compared to the null model (Table 3). More fish were caught when the concentration of dissolved oxygen in the water was lower (Figure 9A). Light intensity was less well supported than models with some of the other variables, but with the AICc being greater than 2 less than the null, there was still strong evidence of it being likely to have an effect. Here, the number of fish caught in a trap increased as light intensity increased (Figure 9B).

Table 3. The $\Delta AICc$ for models explaining the total number of fish caught per trap.

Models differ in the explanatory variable included, and all include trap location nested within pond site as the random effect. The null model has no explanatory variable, only the random effects. Models with environmental variables include those variables recorded at each trap location. Week (week 1-13) and morning or afternoon (sampling in AM or PM) represent when data collection occurred.

Explanatory variable	$\Delta AICc$	d.f
Week	0	5
Dissolved oxygen	18.5	5
Temperature	27.5	5
Light intensity	31.3	5
Null model (no explanatory variables)	35.6	4
Morning or afternoon	36.2	5
Turbidity	37.6	5

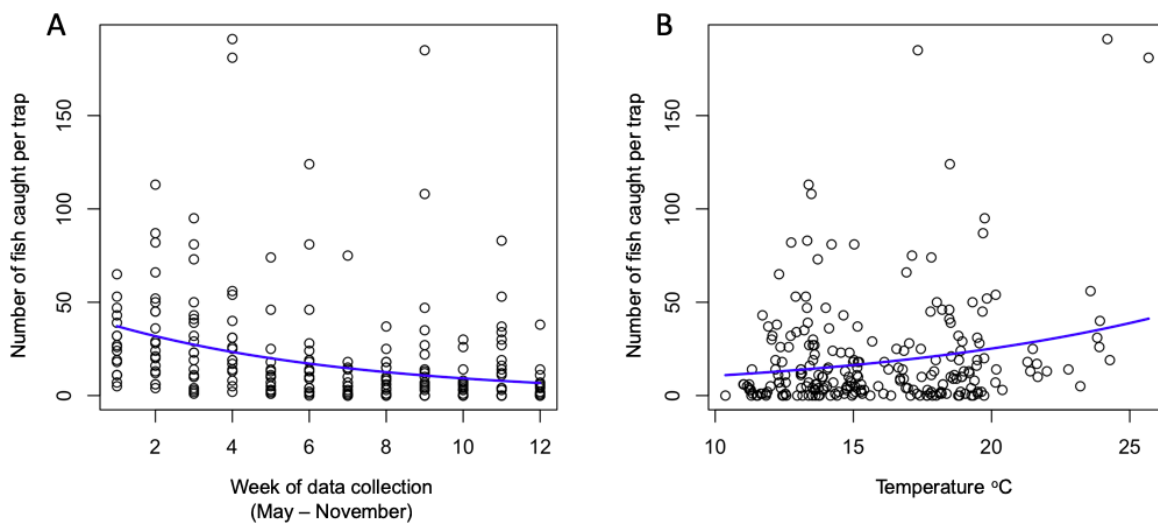


Figure 8. The number of fish caught per trap as a function of (A) the week of data collection and (B) the water temperature at each trap location. Plotted lines show the fitted relationships from GLMM coefficients.

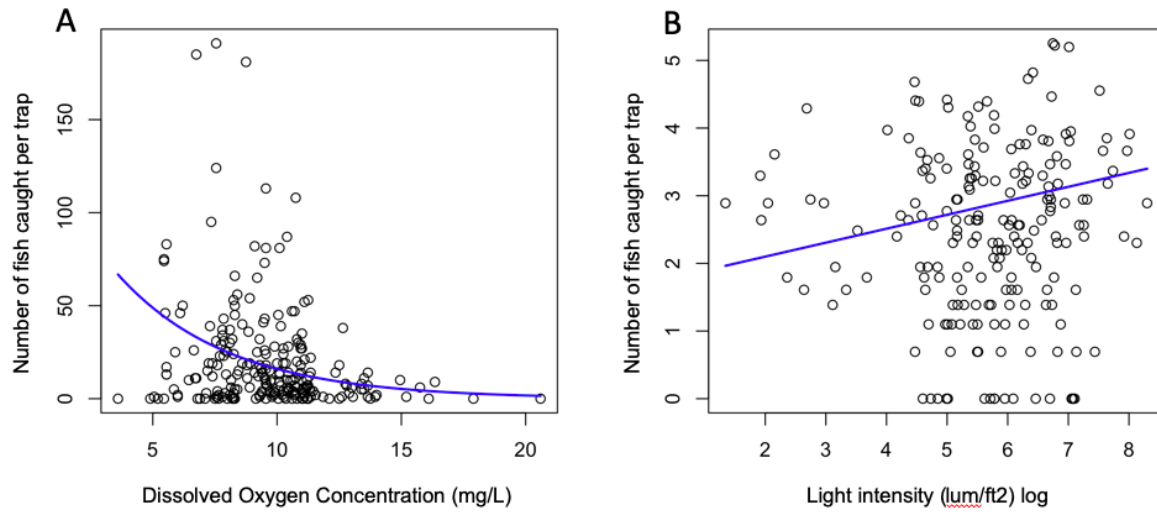


Figure 9. The number of fish caught per trap as a function of (A) the concentration of dissolved oxygen and (B) the light intensity at each trap location. Plotted lines show the fitted relationships from GLMM predicted values.

Aggregation of fish

When testing the variables that predict the aggregation of fish across the traps at each site visit, the best model given the data was the model with the proportion of red-bellied males as the explanatory variable (Table 4). The proportion breeding-condition males was negatively associated with the aggregation score (Figure 10). All other models had larger AICc values than the null model so were not supported by the data.

Table 4. The Δ AICc for models explaining the aggregation of fish.

Models differ in the explanatory variable included, and all include pond site as the random effect. The null model has no explanatory variable, only the random effect. Week (week 1-13) and morning or afternoon (sampling in AM or PM) represent when data collection occurred. Proportion of red males caught represents how many breeding-condition males were caught relative to the total number caught.

Explanatory variable	Δ AICc	d.f
Proportion of red males caught	0	4
Null model (no explanatory variables)	2.6	3
Dissolved oxygen	3.3	4
Morning or afternoon	3.5	4
Turbidity	4.0	4
Temperature	4.9	4
Week	4.9	4
Light intensity	5.0	4

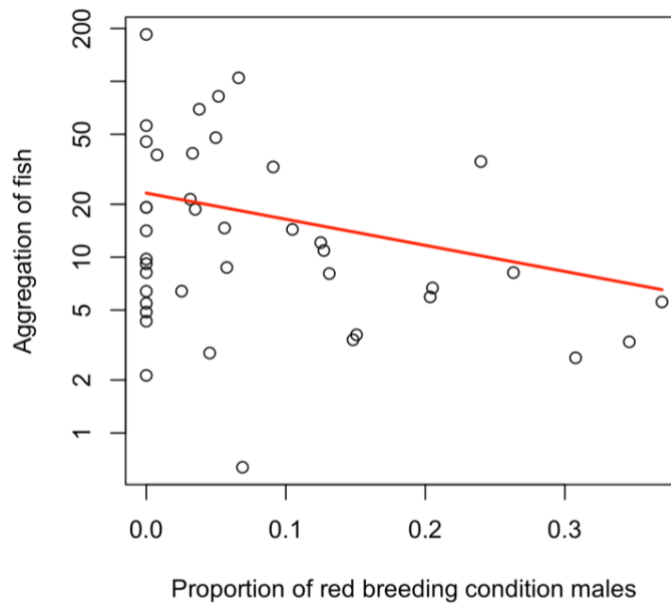


Figure 10. Relationship between the proportion of red-bellied males caught and the aggregation of fish. Plotted line shows the fitted relationship from GLMM coefficients.

Body size assortment of shoaling fish

The lengths of fish caught in traps ranged from a maximum size of 70 mm and minimum size of 16 mm (39.3 ± 8.4 mm, mean \pm SD, $n = 4814$ individuals). We found little evidence of body length assortment among the fish caught in the traps. Out of 44 quantiles, calculated for each site visit (where 8 visits were unsuitable for analysis due to low numbers of fish caught during the visit or the distributions of fish across traps), only 1 quantile was below <0.025 (Figure 11A). The majority of visits yielded non-significant tendencies to be positively assorted (e.g. Figure 11B); in 8 of the 44 visits, the values tended towards negative assortment (e.g. Figure 11C) but none were statistically significant.

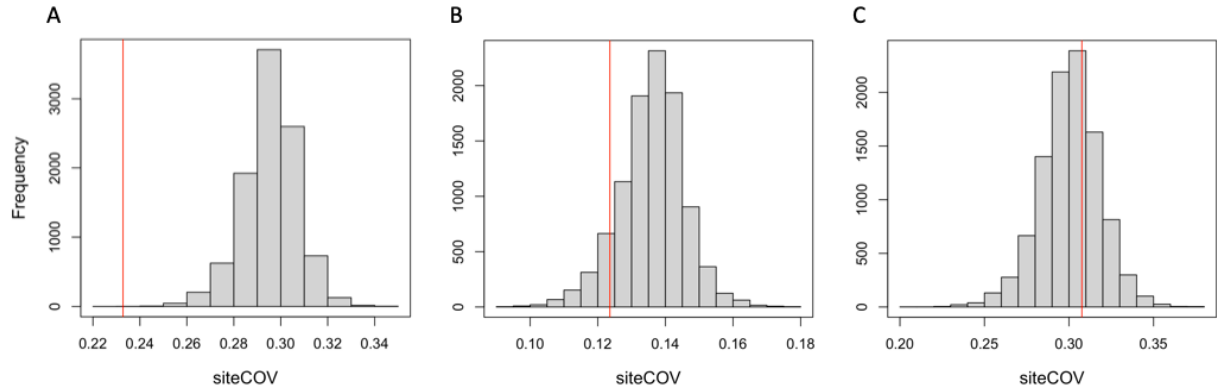


Figure 11. Example expected distributions generated by randomised sampling for three site visits. Red line shows observed value, i.e. the median of the COV for that site visit. Examples of (A) the statistically significant value for positive assortment (quantile 0.004), (B) a non-significant value for positive assortment (quantile 0.195) and (C) a non-significant value for negative assortment (quantile 0.68).

Discussion

Fewer fish were caught over the weeks of data collection, likely a result of the changing seasons, where more fish were caught in spring and summer, declining through autumn and into winter. This is supported by the correlation between consecutive site visits and decreasing temperature and light intensity. Similarly, fewer fish were caught with decreasing temperatures. This can be explained by fish being ectothermic and having lower metabolisms at lower temperatures (Clarke and Johnston, 1999); therefore, in colder weather they are expected to be less active (Bartolini *et al.*, 2015) and have a lower need to explore their environment looking for food (Clarke and Johnston, 1999). We found weaker evidence for reduced light intensity causing less fish to be caught. This trend could be attributed to the correlation between temperature and light intensity, where increased light intensity results in increased temperatures, and in turn increased temperature led to more fish being caught (Ilha *et al.*, 2018).

The trend between the numbers of fish caught through the weeks of data collection and with decreasing temperatures was maintained when considering environmental variation at trap locations. However, this within-site variation revealed evidence for light intensity and dissolved oxygen to be impacting the numbers of fish caught. For light intensity, this could be a result of differences in canopy cover at different trap locations (canopy cover was not recorded) (Ilha *et al.*, 2018). Additionally, fewer fish were caught in areas with a higher dissolved oxygen concentration. As dissolved oxygen concentration was not correlated with temperature or the week of data collection, its effect cannot be attributed to these variables. The effect only being found when considering differing oxygen concentrations within a pond site, i.e. from different trap locations, suggests fish respond to small-scale variation in oxygen concentration at the different trap locations. The effect not being found at the site level could be due to a lack of variability in dissolved oxygen concentrations between site visits. In contrast to our results previous studies have shown fish are less active at lower oxygen concentrations; however, unlike these studies, the oxygen levels we have recorded are not low enough to be detrimental to the point where they would cause stress (Kramer, 1987). For example, Moss and McFarland (1970) only found measurable changes when near-lethal oxygen levels were reached or levels dropped rapidly, whereas our sites had consistent changes within normal boundaries, which may explain why we find this contrary effect. One possible explanation for this result is that dissolved oxygen concentration is correlated with other parameters we did not record (Rydberg *et al.*, 1990; Hagy *et al.*, 2004).

Sticklebacks were less aggregated when the proportion of red-bellied breeding condition males caught was higher, indicating they are being less social during the breeding season. When in breeding condition male sticklebacks maintain territories, in which they build and defend nests

where females are courted to lay eggs (Tinbergen, 1952). As a result of these behaviours, male sticklebacks are more solitary when in breeding condition and more aggressive towards each other, with agonistic behaviours increasing through the breeding cycle (Huntingford, 1976; Kynard, 1978). This would explain why sticklebacks were less aggregated when more of these males were present. We did not find that aggregation was related to any of the environmental variables we recorded, unlike laboratory-based studies testing a range of environmental variables (Domenici *et al.*, 2002; Bartolini *et al.*, 2015; Chamberlain and Ioannou, 2019; Fisher *et al.*, 2021). This may be because under field conditions with variation in multiple, possibly interacting, environmental parameters, the effects of any single stressor is difficult to detect in comparison to highly-controlled laboratory studies. This may also explain why the week of data collection was also not related to aggregation, while repeatedly testing shoals of sticklebacks under laboratory conditions does show a reduction in aggregation over time (MacGregor and Ioannou, 2021).

We found little evidence for phenotypic assortment by body size in these stickleback populations. This may be a result of low predation pressure in these sites (Croft *et al.*, 2009), however this is not something we measured. An additional explanation is that when populations are small in number and density, fish face a trade-off between being in a large group with many dissimilar individuals or small groups with few assorted individuals. In this case, the benefits of being in a larger group could outweigh the benefit of being in an assorted one, resulting in a lack of size assortment. It is also possible that more than one shoal were caught in a trap during the 2 hours trial time, where each shoal was assorted but there was no assortment between different shoals caught in the same trap (i.e. shoals were not more likely to enter a trap already containing a shoal that had a similar, compared to a dissimilar, body size distribution). Considering this, future use of our sampling method could be adapted to focus on measuring

assortment by altering the amount of time traps are left in the water, or by coupling the method with video recording when fish enter. Video recordings could be used to exclude cases where multiple shoals have entered the trap within a sampling period from the analysis of assortment, or live monitoring via video could be used to remove the traps once a shoal has entered.

While in this study our pond sites were predominately comprised of stickleback populations, in different sites the method could present problems based on a lack of specificity in which fish species are caught in traps. This can be remedied to an extent by adjusting the size of opening where sympatric species are different in size, but the size disparity between species may not be large enough, and small openings may disproportionately discourage shoals from entering. However, this could also present an opportunity to investigate social behaviour in mixed-species fish shoals (Ward *et al.*, 2002), by comparing the proportions of each species found in each trap to population-level proportions of each species and environmental parameters. Limitations may also occur when considering the size of shoals, where very large shoals may span multiple trap locations and be caught in multiple traps. This can be altered by changing the distribution of traps to be further apart, but will come with its own caveats, for example the ability to deploy traps that are far apart in quick succession. Therefore, problems arise if planning to use our method in, for example, the open ocean, where fish form schools that cover large areas.

A possible source of bias in our method is for certain behavioural characteristics to be over- or under-represented due to using passive traps (Wilson *et al.*, 1993; Biro and Dingemanse, 2009). Kressler *et al.* (2021) found that when using passive traps, more active fish were captured sooner, and counter-intuitively, when traps contained conspecifics, less-social fish were also captured sooner. This is something to be considered, and could even provide an interesting

opportunity for further work using this method, to explore personality of the sampled fish in the context of sociality and changing environments. A related issue is the novelty of traps (Wilson *et al.*, 1993; Michelangeli *et al.*, 2016; Kressler *et al.*, 2021), but because we were resampling the same sites over months with the same traps, it is likely that the traps are no longer considered to be a novel stimulus. As fewer fish were captured over the weeks of data collection, it could be inferred that sticklebacks are learning to avoid the traps over time. Again, this could be examined in future work; observations of how the fish enter traps and whether they appear to actively avoid them would be necessary to suggest that sticklebacks are learning to not enter traps.

In future applications, this method could be used to compare sites with distinct differences, for example, polluted versus pristine environments. The effects of environmental factors other than the ones we have looked at here, such as chemical pollutants (Michelangeli *et al.*, 2022) or anthropogenic noise (Sarà *et al.*, 2007; Purser and Radford, 2011; Voellmy *et al.*, 2014a; 2014b), could also be investigated, as well as considering multiple stressors (Ormerod *et al.*, 2010; Ginnaw *et al.*, 2020). Additionally, hypotheses could explore more biotic factors in the environment, such as predation risk (Ioannou, 2021) or invasive species (Strayer *et al.*, 2006). In the case of invasive species, the association of native and invasive species within traps could be used to infer whether these species are interacting socially or are avoiding one another (Camacho-Cervantes *et al.*, 2014), and whether environmental parameters affect these interactions (Glitzbecker *et al.*, 2015).

Here we have established a novel field method for investigating the impacts of environmental variation on social behaviour in fish. Our results demonstrate the validity of the method, presenting trends that we would expect to find in stickleback populations based on breeding

condition and external abiotic factors. This method has some substantial benefits over other techniques, particularly being cost-effective and feasible practically. However, it does come with caveats relating to the size of groups, species, and other potential biases which may be revealed through further investigation. Nevertheless, it provides an opportunity to investigate hypotheses regarding fish social behaviour under environmental change, anthropogenic pollution, and other biotic factors under field conditions, questions which to date have been dominated by experimental laboratory studies (Fisher *et al.*, 2021).

Chapter 3

Investigating the impacts of acoustic noise on group dynamics in guppies (*Poecilia reticulata*)

Abstract

Group-living has essential fitness benefits for many species. A central component of group-living is how decisions are made in a social context, which can be altered by individual states and environmental context. Anthropogenic impacts can alter environmental conditions, reducing access to information and signals used for effective group decision-making. Anthropogenic noise pollution is a growing concern, particularly in aquatic environments, due to its impact on accessing information. In this study, we assess how anthropogenic noise impacts the group decision-making, cohesion and activity of fish shoals, using Trinidadian guppies (*Poecilia reticulata*) as a model species. Individual movements within a radially-symmetric five-armed maze were measured using high resolution trajectory data from video tracking software. The behaviour of groups with and without continuous acoustic white noise were measured over a four-day testing period in a repeated measures design. We found no change in individual swimming speed with additional noise, however they became slower and more exploratory (i.e. made more movements into arms) over the four-day period. Cohesion did not change as a result of added noise, nor over the testing period. A greater proportion of the moves into arms were leadership attempts (moves into empty arms) in the added noise treatment compared to the control; not because there were more leadership attempts in the noise treatment but because there were fewer following events (moves into arms occupied by another individual). We found strong evidence for consistent, repeatable differences between groups in all of our behavioural parameters indicating strong personality variation at the group level. These results provide novel evidence for how anthropogenic noise can alter decision-making dynamics in fish shoals, even when group cohesion and activity remain consistent.

Introduction

Group-living has important fitness benefits that can improve foraging (Ranta and Kaitala, 1991), efficiency of movement (Svendsen *et al.*, 2003; Marras *et al.*, 2015), and avoiding predators (Ioannou, 2021). These benefits are often mediated by social interactions that allow for information transfer between individuals (Couzin *et al.*, 2005). Group-living also has costs (Krause and Ruxton, 2002), and whether or not conformity is favoured by individuals to maintain group cohesion can depend on individuals fitness requirements (Herbert-Read *et al.*, 2011).

Some of the benefits provided by group-living are maintained by collective decision-making, where deciding collectively improves the ability of individuals to exploit resources and evade predation (Torney *et al.*, 2009; Ward *et al.*, 2011; Dussutour and Nicolis, 2013). Group decisions may be egalitarian, where decisions are equally shared among individuals, or involve leadership by a few individuals within a group, or even by a single individual (Burns *et al.*, 2012; Nagy *et al.*, 2013; Strandburg-Peshkin *et al.*, 2015; Herbert-Read *et al.*, 2019). Fish shoals are thought to use cues based on the location and movement of other individuals, rather than active signals, to mediate collective movement (Ioannou *et al.*, 2011; Lemasson *et al.*, 2018). Leaders emerge through positional changes within a group, with those at the front of a shoal having more influence over the direction of movement (Bumann and Krause, 1993; Krause *et al.*, 2000).

Individual traits have been shown to impact who contributes to decisions made in a group (Fischhoff *et al.*, 2007; Brown and Irving, 2014; Pettit *et al.*, 2015; Ioannou and Dall, 2016). The tendency to lead can depend on individual personality traits like boldness (Reebs and Leblond, 2006; Harcourt *et al.*, 2009), or traits such as sex, size and reproductive or nutritional

state (Krause *et al.*, 1992; Fischhoff *et al.*, 2007; del Mar Delgado *et al.*, 2018; Garland *et al.*, 2018). Individuals within a group will also have different information which can cause them to exert more influence over group decisions, e.g. about the location of resources (Ioannou *et al.*, 2015), or have disparate motivations as a result of variation in degrees of risk perception (McDonald *et al.*, 2016).

While studies of the mechanisms of collective decision-making and how individual heterogeneity can alter its dynamics are extensive, the impacts of ecological contexts are less well known. Evidence that group decision-making can change with ecological conditions has been demonstrated in guppy shoals, where Ioannou *et al.* (2017) found that group decision-making differed depending on whether individuals were caught from a low- or high-predation river (Ioannou *et al.*, 2017). However, there have been relatively few empirical studies of how abiotic conditions affect the dynamics of group decision-making. Chamberlain and Ioannou (2019) found that with experimentally induced turbidity three-spined sticklebacks (*Gasterosteus aculeatus*) shifted their behaviour away from that of the group and favoured independent decision-making. Here, sticklebacks lost the benefits provided by collective decision-making due to the visual constraints imposed by turbidity (Chamberlain and Ioannou, 2019).

Abiotic environmental conditions have been shown to affect individual and social behaviour in various ways (Fisher *et al.*, 2021). Signals and cues in a suboptimal environment deteriorate, constraining the sharing of information between individuals (Fisher *et al.*, 2021). Abiotic conditions can also directly influence the sensory systems animals use to perceive information (Scott and Sloman, 2004; Fisher *et al.*, 2021). This disrupts the sharing of information between individuals, which can in turn have consequences for group-living (Fisher *et al.*, 2021). Having

reduced social information can lead individuals, and therefore groups, to make worse decisions due to a restricted ability to gather information. For example, in turbid conditions sticklebacks were less likely to favour larger shoals, due to a restricted sensory ability to assess size and quality of groups (Fischer and Frommen, 2013).. As a result, environmental pollutants can disrupt the cohesion of animal groups and alter social interactions by preventing efficient communication between group members (Fisher *et al.*, 2021).

Anthropogenic noise pollution is a growing concern, particularly in aquatic environments (Slabbekoorn *et al.*, 2010). Human activities including ship traffic, construction, tourism and recreation have increased significantly over the past century, and with them so has anthropogenic sound (Peng *et al.*, 2015). Due to the properties of sound waves, noise can travel further and with less deterioration in water than in air, meaning the impacts of noise pollution are spread further (Slabbekoorn *et al.*, 2010). Animals use acoustic signals for communication and to gather information about their environment. Anthropogenic noise can therefore mask this information by decreasing the signal to noise ratio (Brumm and Slabbekoorn, 2005; Wysocki and Ladich, 2005; Vasconcelos *et al.*, 2007; Codarin *et al.*, 2009). Noise can also distract individuals from important fitness tasks, such as foraging (Purser and Radford, 2011; Voellmy *et al.*, 2014a), and cause direct stress (Smith *et al.*, 2004; Wysocki *et al.*, 2006).

These impacts of acoustic noise pollution can have knock on effects on social behaviour (Nowacek *et al.*, 2007; Tyack, 2008). Cetaceans have been found to alter their calls as a result of boat noise, in frequency (Parks *et al.*, 2007) and duration (Foote *et al.*, 2004), demonstrating that acoustic noise disrupts acoustic communication between marine mammals (Fisher *et al.*, 2021). The distraction and stress effects of noise can also disrupt collective behaviour through cross-modal effects, where the effective use of information is impaired by additional noise

(Morris-Drake *et al.*, 2016). These processes are likely to be disrupted when individuals are experiencing distraction and stress. Noise has been shown to reduce the coordination and cohesion of shoals (Sarà *et al.*, 2007; Herbert-Read, Kremer, *et al.*, 2017). However, whether noise disrupts the decision-making processes of fish shoals has yet to be addressed.

Here, we aim to investigate how acoustic noise impacts behaviour parameters and group dynamics of fish shoals using Trinidadian guppies (*Poecilia reticulata*) as a model species. The design was adapted from Ioannou *et al.* (2017) to explore how activity, cohesion and collective decision-making change with noise disturbance compared to a control. Using a five-arm radially symmetrical maze tank, groups were presented with quantifiable choices, i.e. which arm to move into, replicating decisions they would have to make in the environment. We recorded groups of guppies swimming in this experimental tank with a playback of either a recording from their housing tank or this recording with white noise overlaid to simulate acoustic noise pollution and test its distraction (Purser and Radford, 2011) or potential stress effects (Wysocki *et al.*, 2006). White noise comprises a broad spectrum of frequencies with equal intensity (Scholik and Yan, 2001) and was used as a treatment to simulate potential acoustic noise disturbances that could occur in a freshwater environment (i.e. by encompassing a range of frequencies white noise is relevant to a range of acoustic noise disturbances). Using a repeated measures design allowed us to also test whether groups varied in their behaviour consistently over the days of testing in the two treatments. Support for this would be evidence of group-level personality (Planas-Sitjà *et al.*, 2015; Salazar *et al.*, 2015; Jolles *et al.*, 2018; MacGregor and Ioannou, 2021).

Materials and Methods

Ethics statement

All experiments were carried out at the University of Bristol aquarium and were approved by the University's Animal Welfare and Ethical Review Body (UNI/17/060 and UNI/17/075). Methods followed ASAB Guidelines for the treatment of animals in behavioural research. Individuals were exposed to a maximum of two 20-minute noise treatments (including the time for habituation and the experimental trial) to minimise exposure to potentially stressful conditions.

Study species

Guppies (*Poecilia reticulata*) were collected from a high-predation site on the Guanapo river in Trinidad, West Indies, in April 2019. They were exported to the John Krebs field station, University of Oxford, and reared for three generations. Guppies were bred under a controlled breeding plan to prevent inbreeding and ensure genetic diversity was maintained. The third generation were moved to the University of Bristol in December 2020. All individuals were kept in 90 litre glass tanks (40 x 70 x 35 cm W x L x H) with approximately 100 to 150 fish per tank. Tanks contained artificial plants, plastic tunnels and a slow bubbling air stone. Water temperature was maintained at 25 ± 1 °C (mean \pm SD). Lighting was maintained on a 12:12 hr light:dark cycle. Fish were fed on a diet of live and fresh food (frozen blood worms, cyclops, mysis, brineshrimp and live banana worms) and ZM Granular pellets (© Copyright 2021 ZM Fish Food and Equipment).

Noise Treatments

Treatments were an ambient control made of a playback of recorded noise from the guppies' housing tank, and a noise treatment of white noise overlaid onto the ambient track. The ambient

track was recorded with a HiTech HTI-96-MIN hydrophone (sensitivity level 6) and a Zoom H1n digital recorder in the experimental guppies original housing tank at half water depth. A 5-minute recording was looped to generate a 30-minute track of ambient sound for the control treatment. The track was in excess of the trial time to allow continuous play while collecting experimental groups. The white noise treatment was generated in Audacity (version 2.4.2) and overlaid onto the ambient sound track to simulate the effect of added anthropogenic noise onto their normal ambient soundscape.

Both playback tracks were 30 minutes in duration to prevent any interruption during the trial period. They were played back from a SanDisk Clip Jam MP3 player through a DNH Aqua-30 underwater loudspeaker (UW-30, frequency response 100-10,000 Hz) connected to an amplifier (Kemo Electronic GmbH; 18 W; frequency response: 40-20 000 Hz) and a Maplin 12 volt battery. The speaker was suspended in a plastic box using elastic to minimise vibrations and this was submerged in the bottom of a 63 x 83 cm black tub, 45 cm below the experimental tank (Figure 12A).

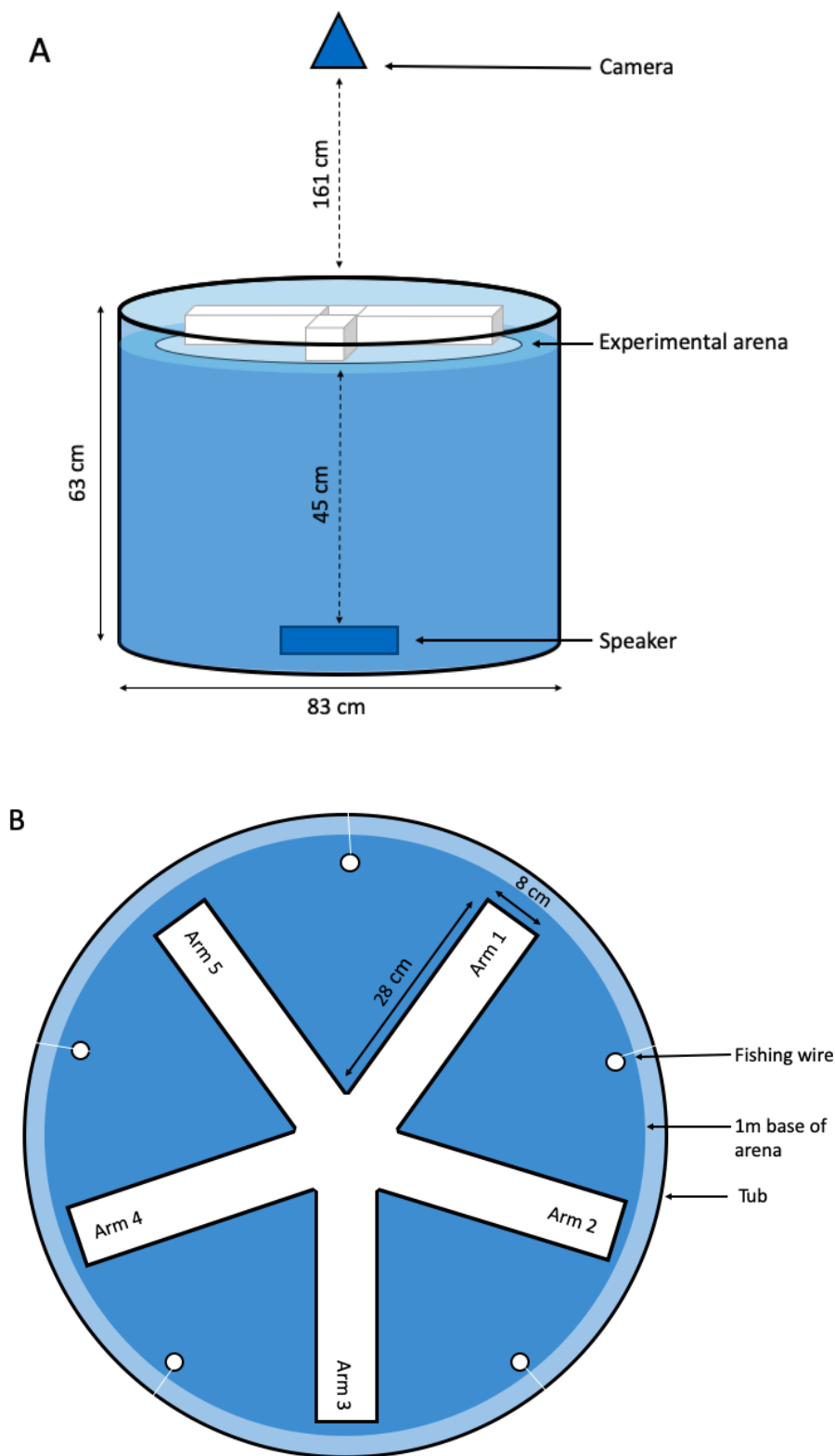


Figure 12. Diagram of the experimental set up. (A) Side view of experimental tank in tub with camera and speaker placement. (B) Overhead view of the experimental tank suspended in the tub by fishing wire. Not to scale.

Tank acoustic analysis

Hydrophone recordings were taken from the experimental tank for both treatments using a HiTech HTI-96-MIN hydrophone and Zoom H1n digital recorder (sensitivity levels: 3 for ambient playback, 5 for white noise playback). 10-second recordings were taken at the end, middle, and start of each arm, and one recording taken in the middle of the experimental tank (Figure 13). The noise level was higher in the middle of the experimental tank due to using playbacks in relatively small tanks. The recorded noise level in the guppies' original holding tank was 107 ± 2 dBs (mean \pm SD), which the ambient control mimicked, with the added white noise treatment being distinctly louder (Table 5).

Table 5. The noise level in decibels for each area of the experimental tank reported as mean \pm standard deviation. F1 refers to the corresponding letters in in Figure 1. Hydrophone recordings were analysed in MATLAB v2013a.

F1	Area of experimental tank	Ambient control treatment dBs	Added white noise treatment dBs
A	Middle of tank	112	138
B	Start of arms	107 ± 0.9	136 ± 1.0
C	Middle of arms	106 ± 1.2	135 ± 1.0
D	End of arms	105 ± 0.6	132 ± 0.7

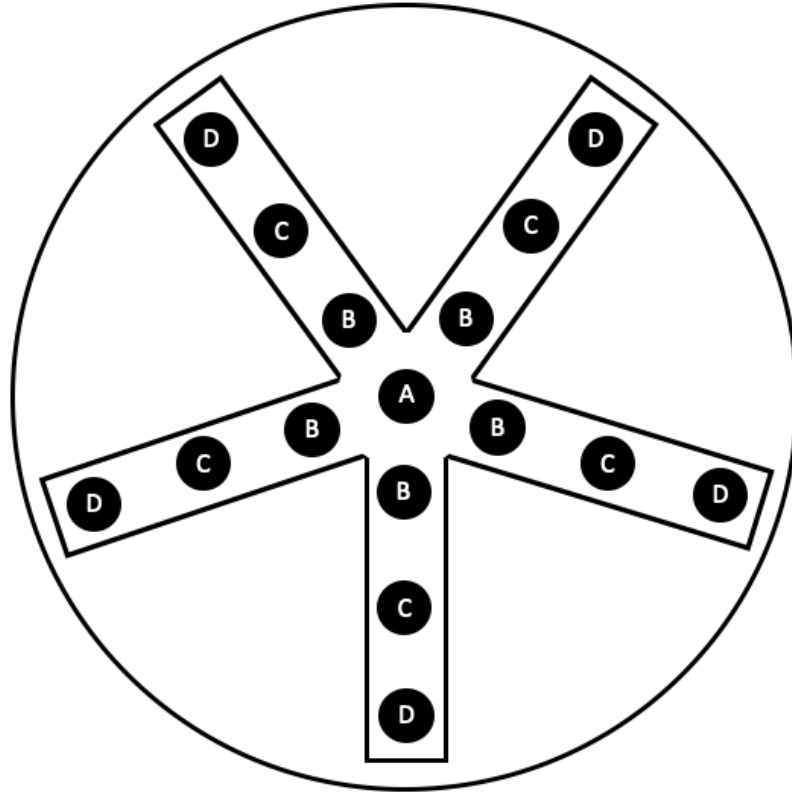


Figure 13. Areas of experimental tank where hydrophone recordings were taken, corresponding to data in Table 1.

To analyse the particle motion in the experimental tank, accelerometer recordings were taken using a M20-40 Geospectrum Technologies Inc. accelerometer and Zoom H6 digital recorder (sensitivity level: 3 for ambient playback, 5 for white noise playback). Recordings were made in middle of the experimental tank and once in each arm. Due to the shallow water depth and relatively large size of the accelerometer, it had to be orientated horizontally and thus could only record on the Z axis. 30-second recordings were taken and these were cropped to 10 seconds for analysis. The range of mean values for particle motion throughout the experimental tank were 30.58 – 81.56 dB re $1 \mu\text{m s}^{-2}$ in the ambient control treatment and 49.66 – 97.99 dB re $1 \mu\text{m s}^{-2}$ in the added white noise treatment (Figure 14).

All acoustic recordings were analysed in MATLAB 2013a using paPAM (Nedelec *et al.*, 2016). A bandpass filter was applied between 100 and 2000 Hz to account for all hearing sensitivities in fish (Popper and Fay, 2011). All heaters and filters were switched off during recordings and water depth and temperature were kept constant, matching experimental tank conditions used during the trials.

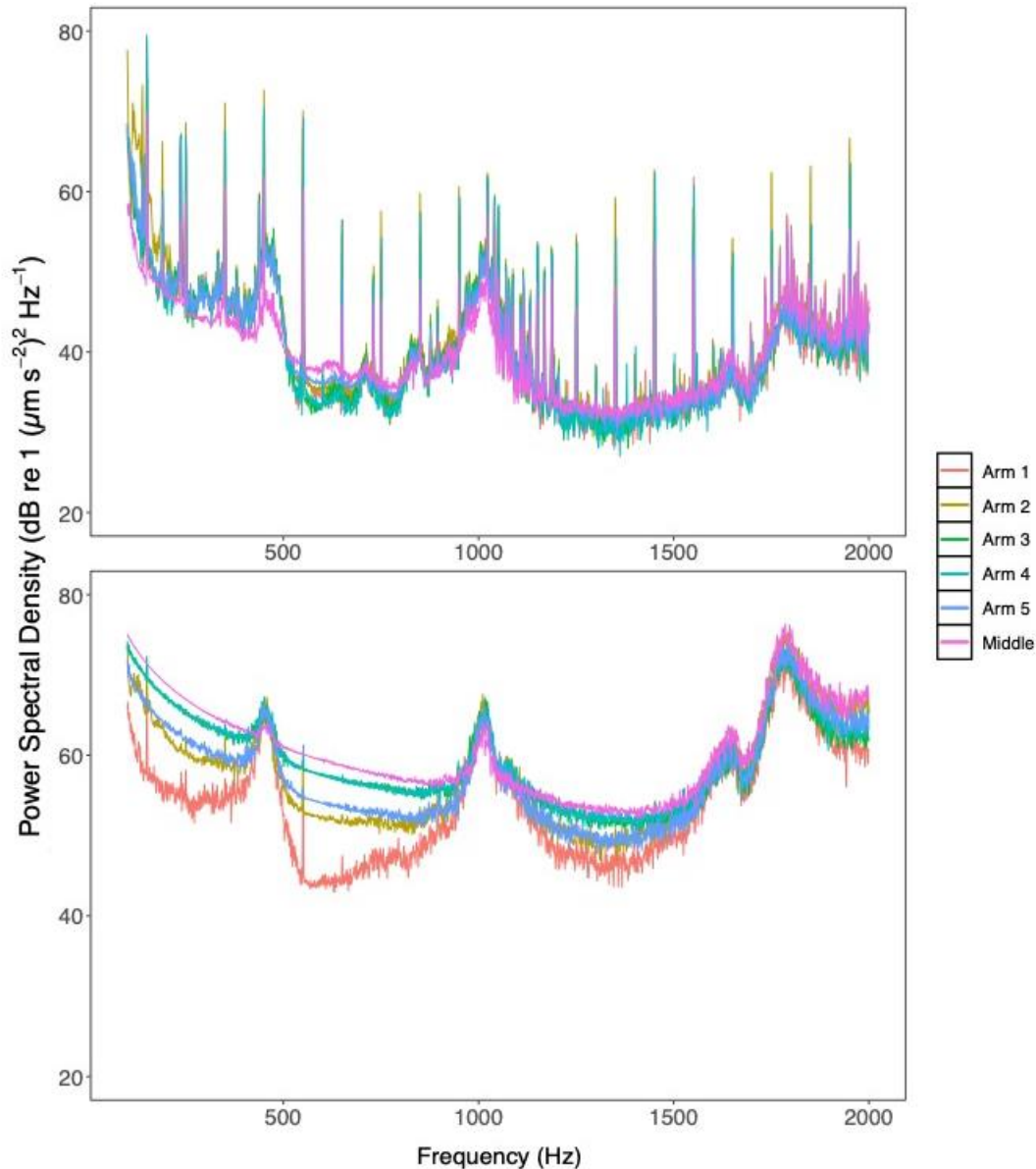


Figure 14. Power spectral density plot for particle motion in each area of the tank for both the ambient control treatment (top) and white noise treatment (bottom).

Water temperature

In order to reduce the noise disturbance in the experimental tank, water heaters (Hepo HP-608 300W Aquarium heaters) and filters (Aquarium Systems Duetto 50 filters) were switched off during trials. To check how much this would affect the water temperature during trials, the experimental procedure was conducted without fish over five consecutive trials: turning heaters off for 20 minutes (the duration of the experimental trials), and on for between five and ten minutes (the time between trials needed to replace the fish tested in the previous trial with the fish to be tested in the next trial). The water temperature in the experimental tank was logged every minute over the 2-hour period using a HOBO MX2202 temperature logger (Figure 15). The temperature fluctuated between 26°C and 26.8 °C, thus remained relatively stable.

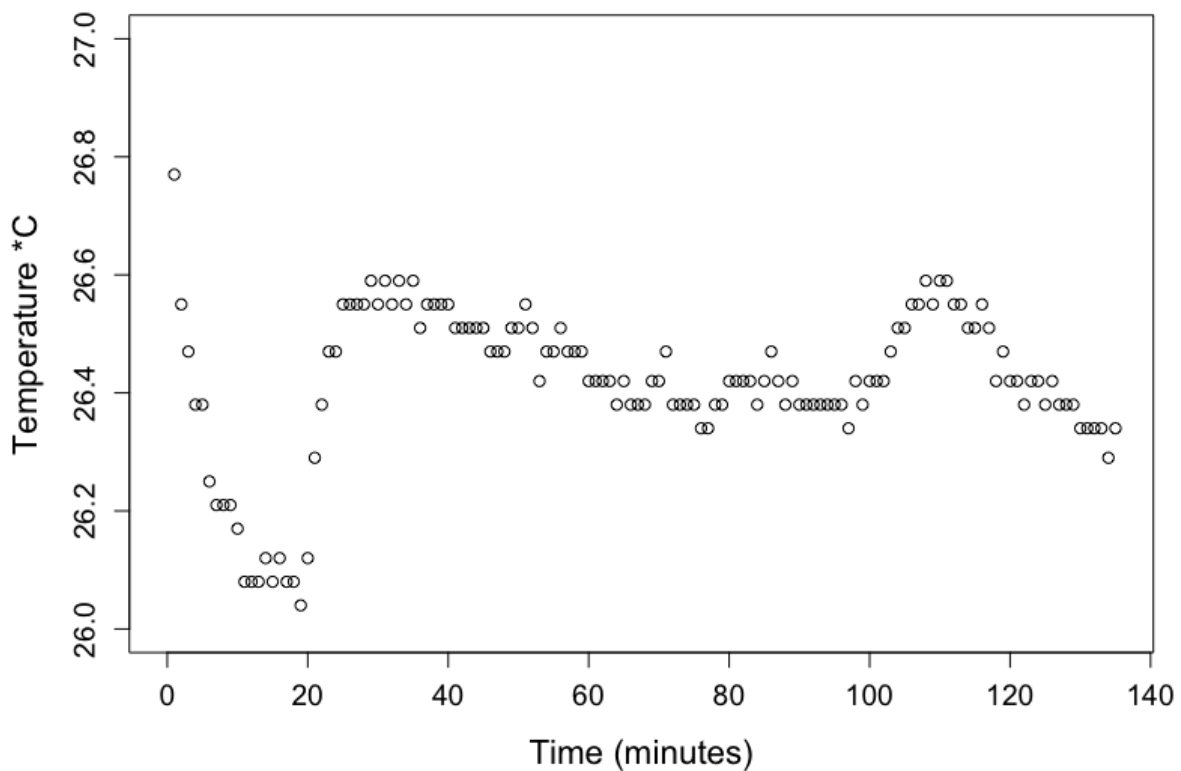


Figure 15. Water temperature in the experimental tank during a simulated five-trial period.

5 Experimental Design

A five-arm maze was constructed out of matt white corrugated plastic. Each arm was 28 x 8 x 18 cm (L x W x H). This was attached with white electrical tape to a 1 m circular base made of white acrylic. The experimental tank was suspended in an 83 x 63 cm cylindrical tub with transparent 8lb fishing wire attached to the base at five points to reduce vibrations (Figure 12A). A Sony AX53 digital 4K video camera recorder was suspended over the tank 161 cm above the base of the experimental tank (Figure 12A). White cotton sheets were suspended around the tank and tub to reduce disturbance to the fish during the trials and to diffuse the overhead fluorescent lighting. An additional piece of black cotton sheet was placed between the lighting and the top of the curtains to reduce glare and reflections on the experimental tank base. The water level in the experimental tank was kept consistent at 7.5 cm. The experimental tank was refilled every day before trials were started, and 50% of the water in the tub was replaced weekly. Water was allowed to fill gaps in the corrugated plastic walls of the experimental tank to prevent air pockets insulating against sound passing through.

Experimental protocol

Groups of four female guppies (29.5 ± 2.4 mm, mean \pm SD, $n = 72$ individuals) were formed of individuals haphazardly caught from the stock tanks 24 hours before the start of the experimental trials. Individuals were randomly assigned to one of 10 groups based on random shuffling the group number (from 1 to 10); one fish was caught at a time using a hand net and assigned to the corresponding group in the randomised order. The group numbers were then reshuffled and the process repeated until four fish were in each group. Groups were formed in this way to minimise potential variation between groups that could be a result of non-random selection, for example if bolder fish are usually caught first (King *et al.*, 2013; MacGregor *et al.*, 2020). Each group was held in a fry nets (16 x 12.5 x 13.5 cm W x L x H) with two per 45

litre tank (20 x 70 x 35 cm W x L x H) in the same room as their original holding tanks. Fish remained in these groups throughout the testing period of 4 days. Fish were fed ZM Granular pellets (© Copyright 2021 ZM Fish Food and Equipment) in the fry nets after being put into groups, and at the end of each day of trials. To control for differences in social and reproductive behaviour of males and females, only single-sex female groups were tested (Croft *et al.*, 2003; Lucon-Xiccato *et al.*, 2016).

All trials took place from Tuesday to Friday between 0900 and 1500 (groups set up on Monday) between 20th September and 5th November 2021. Groups were tested once a day over four consecutive days in a repeated measured design, where the treatment alternated from one day to the next so all groups were tested twice in each treatment (noise or control), where a treatment trial one day would be followed by control trial the next day, and vice versa. Treatment order was decided by random shuffling of group numbers on the first day of testing. The first half of the random list were given the control treatment first and the second half given the noise treatment first. The testing order of groups within a day was also randomised. All randomisation was done using R (version 4.1.2; R Core Team, 2017) in RStudio (version 2021.9.1.375; RStudio Team, 2020).

At the start of a trial the appropriate playback track was played through the underwater speaker and all heaters and filters were turned off. The groups of four fish were transferred to the experimental tank by hand nets and given a three-minute acclimation period inside a 12 x 30 cm clear cylinder made of 5 mm rigid acrylic (Figure 16) in the middle of the tank. At the end of the acclimation period the camera recording was started, the tube was carefully lifted out of the tank with a 75 cm clear rod attached to the tube with fishing wire, the curtains were closed and a 15-minute timer was started. After the 15-minute trial period the camera filming was

stopped, the fish were caught and placed back into their fry net (unless it was the final day of testing, when they were released into a new home tank for fish already used in the experiment), heaters and filters were turned on for the period between the trials, and the experimental tank was set up for the next trial.

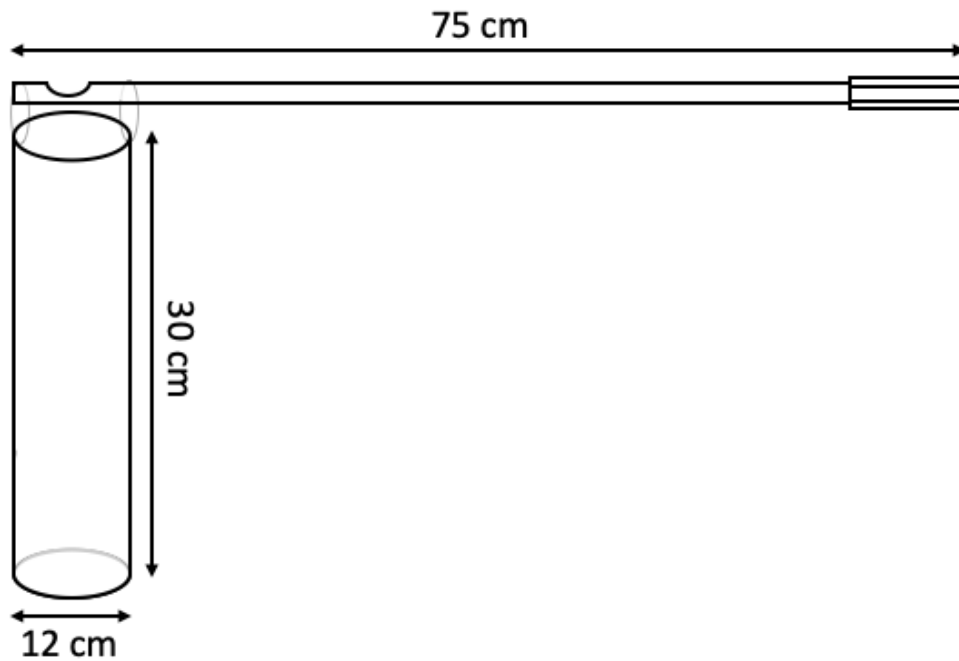


Figure 16. Diagram of acclimation tube and attached rod. Not to scale.

Video analysis and data processing

Video files were recorded in 3840 x 2160 pixel resolution with a frame rate of 25 fps. The automated tracking software idTracker (Pérez-Escudero *et al.*, 2014) was run in MATLAB 2014a to obtain the trajectories of individual fish during the trials at each video frame. Identities were maintained for each trial but could not be confirmed across trials of the same group. idTracker settings used were: number of individuals 4, intensity threshold 0.8, number of frames for references 5000 and minimum size 250. Trajectories were then processed in R (version 4.1.2; R Core Team, 2017). In cases where there were missing coordinates for any individual in a frame, all data were removed from that frame. This is because with missing

information for any given individual, social parameters cannot be reliably calculated. Trajectories were smoothed using a Savitsky-Golay filter using the *Trajr* package in R (version 1.3.0; McLean and Skowron Volponi, 2018). Additionally, when the speed of an individual exceeded 25 pixels per frame, all data points for that frame were removed as this speed was assumed to be a result of erroneous tracking (Figure 17). All trials were cropped to 13.5 minutes each, removing the first 1.5 minutes of the trial where the fish would often remain still after removal of the habituation tube. Overall, we obtained tracked video footage for 72 trials across 18 groups.

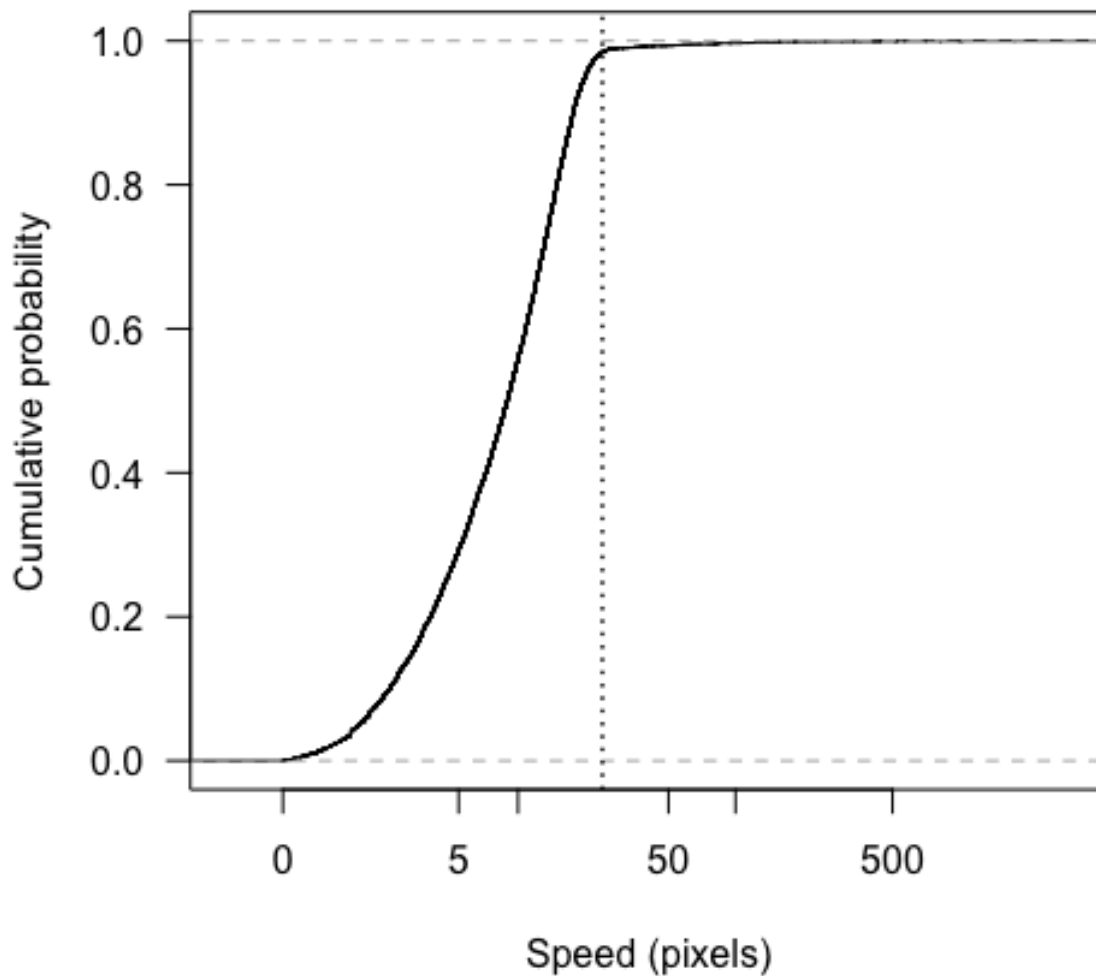


Figure 17. Example of a cumulative density plot for the speed of one individual within one trial. Cumulative density plots were used to determine the threshold at which high speeds were considered erroneous and removed. Vertical dotted line is speed = 25 pixels/frame.

Behavioural parameters

Using the processed trajectory data we calculated the mean speed of individuals across each trial (pixels/frame), and calculated the mean across the four fish of these mean speeds. Which arm each fish was in at every frame, or whether they were in the middle area joining the arms, was determined using the coordinates of the corners of each arm, with the coordinates measured using ImageJ version 1.53 (Schneider *et al.*, 2012). From this four behavioural

parameters were calculated per trial: mean cohesion (the standard deviation of the number of fish in each arm at each frame, averaged (mean) across all frames), the number of leadership attempts (moves into an empty arm), the number of following events (moves into an arm already occupied by another individual), and the total number of moves made into each arm (the sum of the leadership attempts and following events). Data for speed, cohesion, and the total number of movements made into arms included 18 groups and 72 trials. During data processing, when distinguishing between whether movements into arms were leadership attempts or following events, four trials were found to have high rates of error. These four trials were removed from analyses relating to the number of leadership attempts or following events, thus include 18 groups and 68 trials.

Statistical analysis

All analyses were conducted using R (version 4.1.2; R Core Team, 2017) in RStudio (R Core Team, 2017; RStudio Team, 2020). Each behavioural parameter was analysed as a response variable in a separate mixed effects model. Mean speed, mean cohesion and the total number of moves into arms were analysed as response variables in linear mixed models (LMM). To analyse the proportion of moves into arms that were leadership attempts rather than following events, the leadership attempts and following events were transformed into a ratio using the `cbind` function in R (number of leadership attempts, number of following events) and this was used as the response variable in a binomial generalised linear mixed model (GLMM). Based on the results from this model of the proportion of moves into arms that were leadership attempts, additional LMMs were constructed with the number of leaderships attempts and the number of following events as separate response variables.

All models included group identity as a random effect and the time of day the trial began (trial start time) as a covariate. The inclusion of treatment (additional noise or ambient control) and day of testing (1 – 4) was varied between models to test for their independent and combined effects. For each response variable, five models were constructed which included either the treatment * day interaction, treatment and day as main effects only, treatment only, day only or neither of these terms as a null model. To determine which explanatory variables were important for explaining variation in the response, we compared the Akaike information criterion values corrected for small samples sizes (AICc) for each model using the Ictab function in R (bbmle version 1.0.24; Bolker *et al.*, 2020). The model with a ΔAICc of zero is that which best fits the data. We considered models with a ΔAICc of greater than two units less than the null model to have strong support, and therefore the fixed effects of the model were considered important in predicting the response variable (Burnham and Anderson, 2002)

To determine whether there was consistent variation over repeated tests in the behavioural parameters among groups not explained by our fixed effects, models were compared for each response variable with and without the random effect of group identity. For each response variable, models included the fixed effects of start time and the interaction term treatment * day. LMMs were compared to linear models without the random effect. The binomial GLMM was compared to a binomial generalised linear model without the random effect. The ΔAICc values were compared for the two models (with and without the random effect) for each response variable and interpreted these as previously described. In tracking individual identities were not maintained across trials, therefore we only tested for repeatability among groups and not individuals.

We tested for multicollinearity by calculating the variation inflation factors (VIFs). None of our models showed strong evidence of multicollinearity ($VIF < 3$ in all cases). All linear models were tested using QQ plots for the assumption of normality and the residuals plotted against fitted values to ensure homogeneity of variance. All LMMs were fitted with maximum likelihood (ML) rather than the *lme4* default restricted maximum likelihood (REML) because models within the comparisons contained different fixed effects (Faraway, 2005; Harrison *et al.*, 2018). All binomial models were tested for under- or over- dispersion using the residual diagnostics for mixed regression models (DHARMA; Hartig, 2019). All mixed models used the R package *lme4* (version 1.1.30; Bates *et al.*, 2015).

Results

Mean speed of individuals

Analysis of the mean speed of individuals showed that the model with treatment and day as main effects only was the best fit given the data, and was 2 AICc units less than the null (Table 6). The model with only day as the explanatory variable was within 0.3 AICc units of the best model and thus has similar predictive power, therefore including treatment did not substantially make the model a better fit. This suggests that the day of data collection had a stronger effect on the mean speed of individuals than treatment. Group speed decreased over the days of data collection (Figure 18).

Further, the model including only treatment as the explanatory variable was within 2 AICc units of the null model ($\Delta AICc = 0.4$), and thus also suggests the effect of treatment on speed is much weaker than that of day (Table 6). Plotting the predicted values shows a small reduction in speed in the noise treatment compared to the control (Figure 18). Adding the treatment *

day interaction does not improve the fit of the model given the data compared to the main-effects only model, thus the effects of treatment and day are independent and additive.

Table 6. The ΔAICc for models explaining variation in the mean of individuals' speed. Models differ in explanatory variables. The null model includes start time as the only fixed effect. All models include group identity as the random effect. Treatment is noise or control, day is the day of testing (1 – 4).

Explanatory variables	ΔAICc	d.f
Treatment + day + start time	0	5
Day + start time	0.3	6
Treatment * day + start time	2.4	4
Treatment + start time	5.3	5
Start time only (null model)	5.7	7

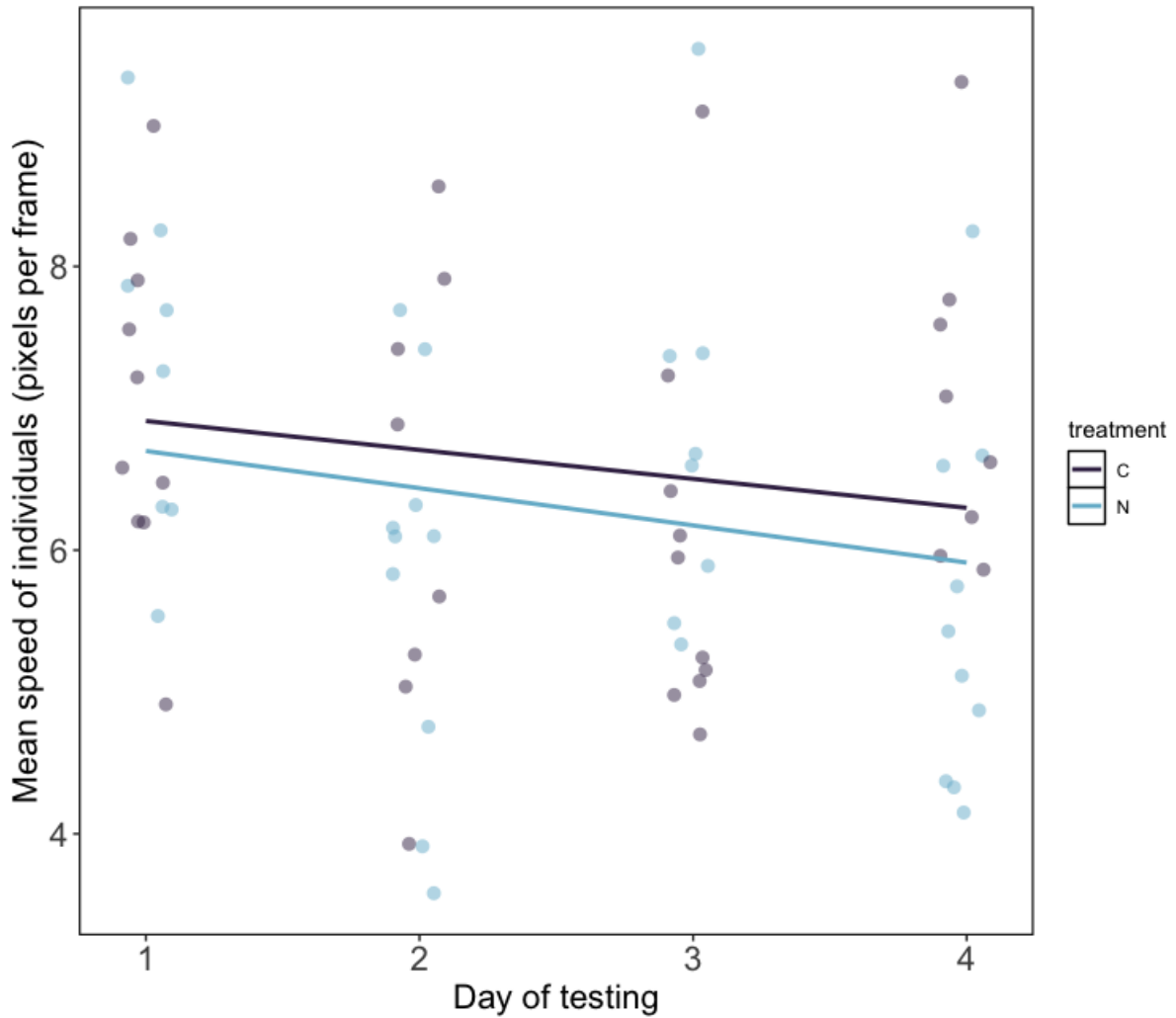


Figure 18. The relationship between the mean speed of individuals and the day of testing in both noise and control treatments. Fitted lines are calculated from LMM fixed-effect estimates from the model with all main effects and the treatment * day interaction term. Points are individual data points (18 groups, 72 trials).

Mean group cohesion

When testing the variables that predicted the group cohesion of fish during trials, the best fitting model given the data was the null model (Table 7). All other models had larger AICc values than the null model so were not supported by the data (Figure 19).

Table 7. The ΔAICc for models explaining variation in the mean group cohesion. Models differ in explanatory variables. The null model includes start time as the only fixed effect. All models include group identity as the random effect. Treatment is noise or control, day is the day of testing (1 – 4).

Explanatory variables	ΔAICc	d.f
Start time only (null model)	0	4
Treatment + start time	0.5	5
Day + start time	0.7	5
Treatment + day + start time	1.1	6
Treatment * day + start time	3.3	7

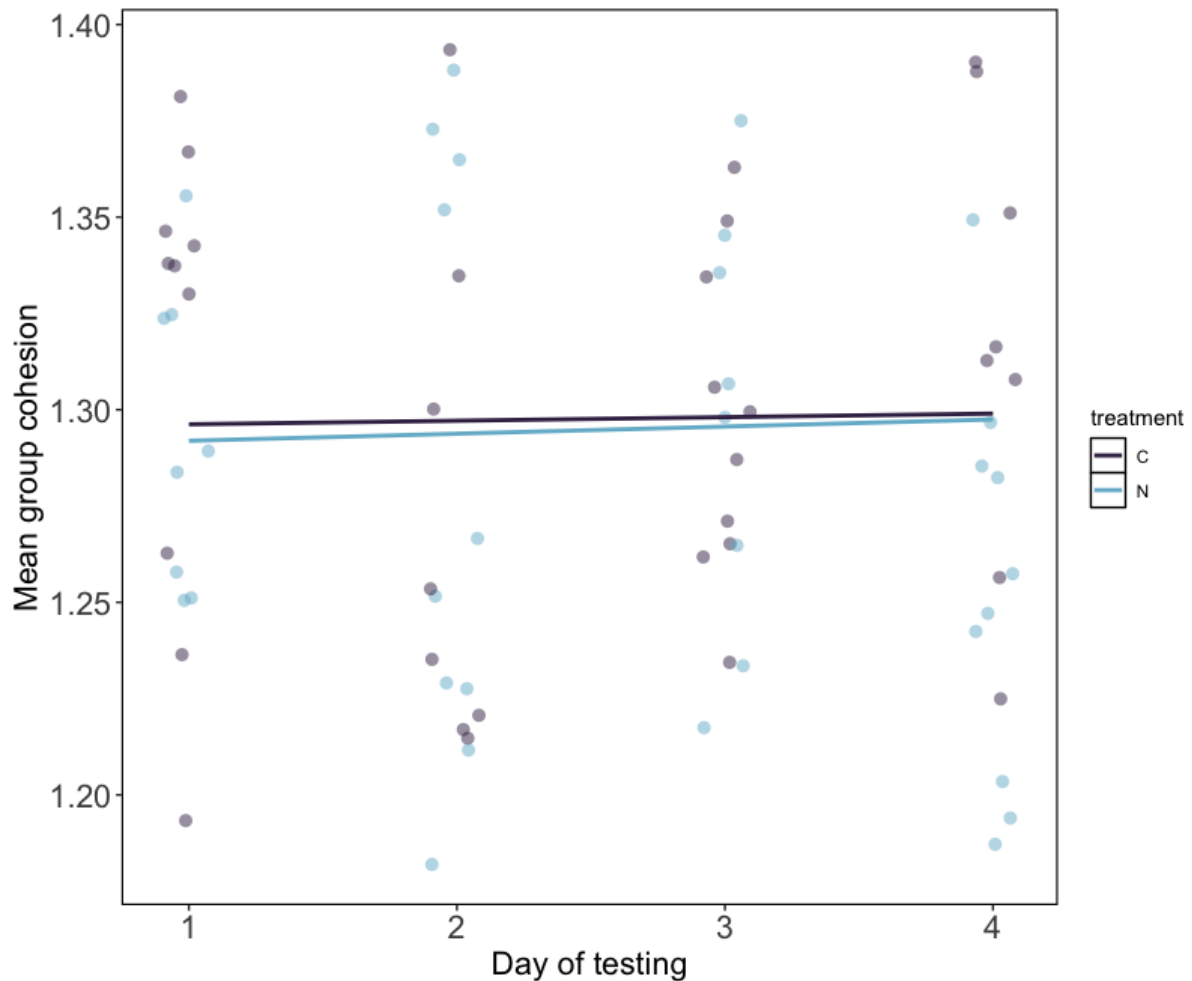


Figure 19. The relationship between the mean group cohesion (standard deviation of the number of fish in the same arm at any time) and the day of testing in both noise and control treatments. Fitted lines are calculated from LMM fixed-effect from the model with all main effects and the treatment * day interaction term. Points are individual data points (18 groups, 72 trials).

Exploration (total number of moves made into arms)

Analysis of the exploration behaviour in the trials (total number of moves made into arms) revealed that the model containing treatment and day as separate main effects was the model with the best fit given the data (Table 8). Within 2 AICc units of this model were the models containing the interaction term of treatment * day ($\Delta\text{AICc} = 0.3$) and only day ($\Delta\text{AICc} = 0.5$) as explanatory variables. Due to these models all having similar AICc values, it can be inferred

that day has the most important effect, since adding treatment or the interaction term of treatment * day does not greatly improve the model fit. The model containing only treatment had a higher AICc value than the null model (Table 8), suggesting that treatment alone had no effect on the exploratory behaviour of groups. Groups were more exploratory as the days of testing progressed (Figure 20).

Table 8. The ΔAICc for models explaining variation in the total number of moves individuals made into arms. Models differ in explanatory variables. The null model includes start time as the only fixed effect. All models include group identity as the random effect. Treatment is noise or control, day is the day of testing (1 – 4).

Explanatory variables	ΔAICc	d.f
Treatment + day + start time	0	6
Treatment * day + start time	0.3	7
Day + start time	0.5	5
Start time (Null model)	5.1	4
Treatment + start time	5.3	5

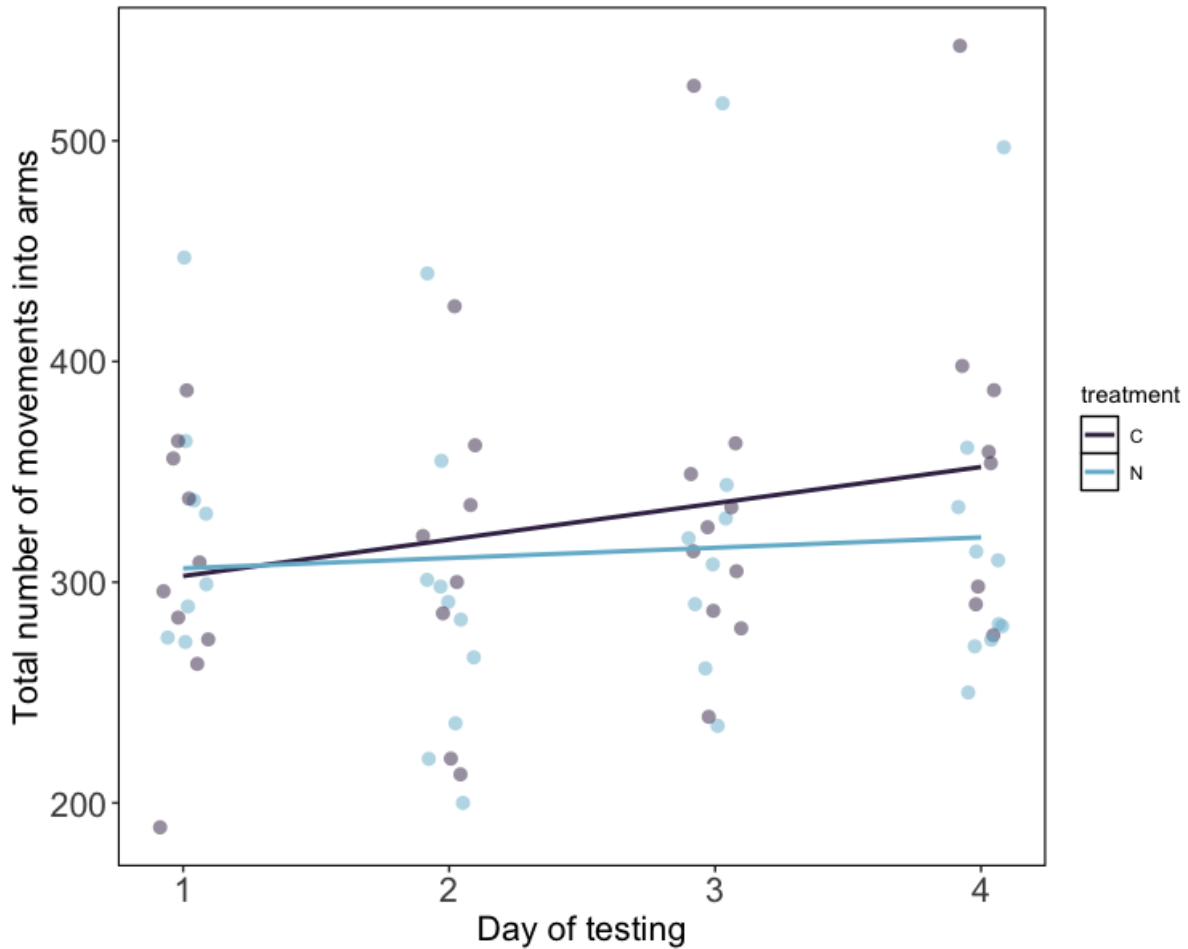


Figure 20. The relationship between the total number of movements into arms during a trial and the day of testing in both noise and control treatments. Fitted lines are calculated from LMM fixed-effect estimates from the model with all main effects and the treatment * day interaction term. Points are individual data points (18 groups, 72 trials).

Proportion of moves into arms that were leadership attempts

When analysing the proportion of moves into arms that were leadership attempts, the model with the best fit given the data was that with only treatment as the explanatory variable (Table 9). Including day in this model did not improve the fit. The model with treatment as the only main effect was 1.9 AICc units below the null model, therefore considered to have moderate

to strong support. Here, there were more leadership attempts in to arms, relative to total movements, in the noise treatment compared to the control treatment (Figure 21).

Table 9. The $\Delta AICc$ for models explaining variation in the proportion of moves into arms that were leadership attempts. Models differ in explanatory variables. The null model includes start time as the only fixed effect. All models include group identity as the random effect. Treatment is noise or control, day is the day of testing (1 – 4).

Explanatory variables	$\Delta AICc$	d.f
Treatment + start time	0	4
Treatment + day + start time	0.3	5
Start time only (null model)	1.9	3
Day + start time	2.2	4
Treatment * day + start time	2.7	6

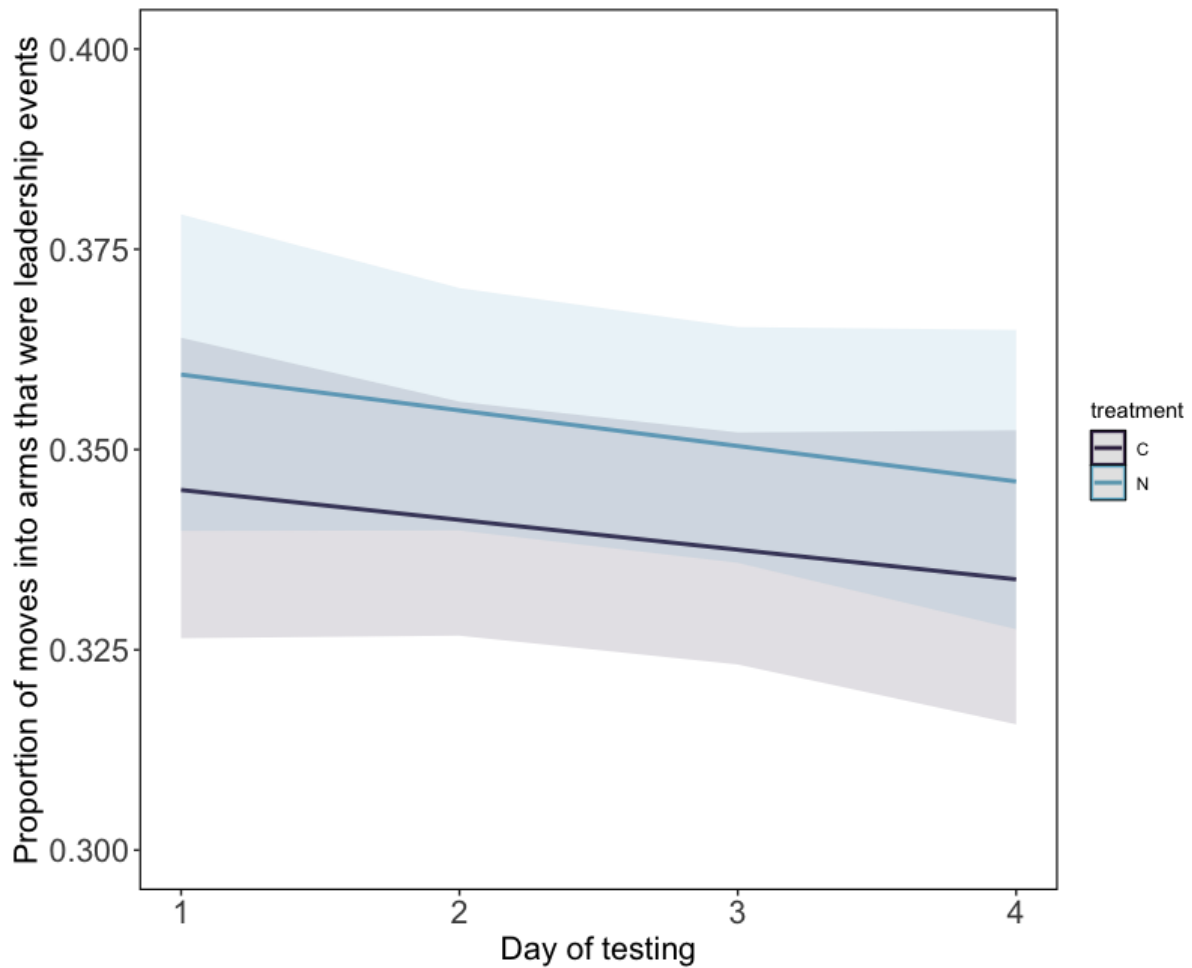


Figure 21. The relationship between the proportion of moves into arms that were leadership events and the days of testing in both noise and control treatments. Fitted lines are calculated from GLMM fixed-effect estimates from the model with all main effects and the treatment * day interaction term (18 groups, 68 trials).

Total number of leadership attempts and following events

First, the number of leadership events were analysed as a response variable and, in a separate model, the number of following events as a response variable. These variables were analysed to determine which, or both, are changing as a function of the noise treatment to affect the proportion of moves that were leadership attempts. Where the number of leadership attempts was the response variable, the best model was that containing only day as a fixed effect. This

was 1.3 AICc units lower than the null, therefore providing some evidence that day has an effect on the number of leadership attempts (Table 10). All other models had AICc values higher than the null and therefore were not supported. Plotting the number of leadership attempts shows a slight increase over the days of testing, similar to the result for the exploratory behaviour of groups (Figure 22).

Table 10. The Δ AICc for models explaining variation in the number of leadership attempts. Models differ in explanatory variables. The null model includes start time as the only fixed effect. All models include group identity as the random effect. Treatment is noise or control, day is the day of testing (1 – 4).

Explanatory variables	Δ AICc	d.f
Day + start time	0	5
Start time only (null model)	1.3	4
Treatment + day + start time	2.2	6
Treatment * day + start time	3.5	7
Treatment + start time	3.5	5

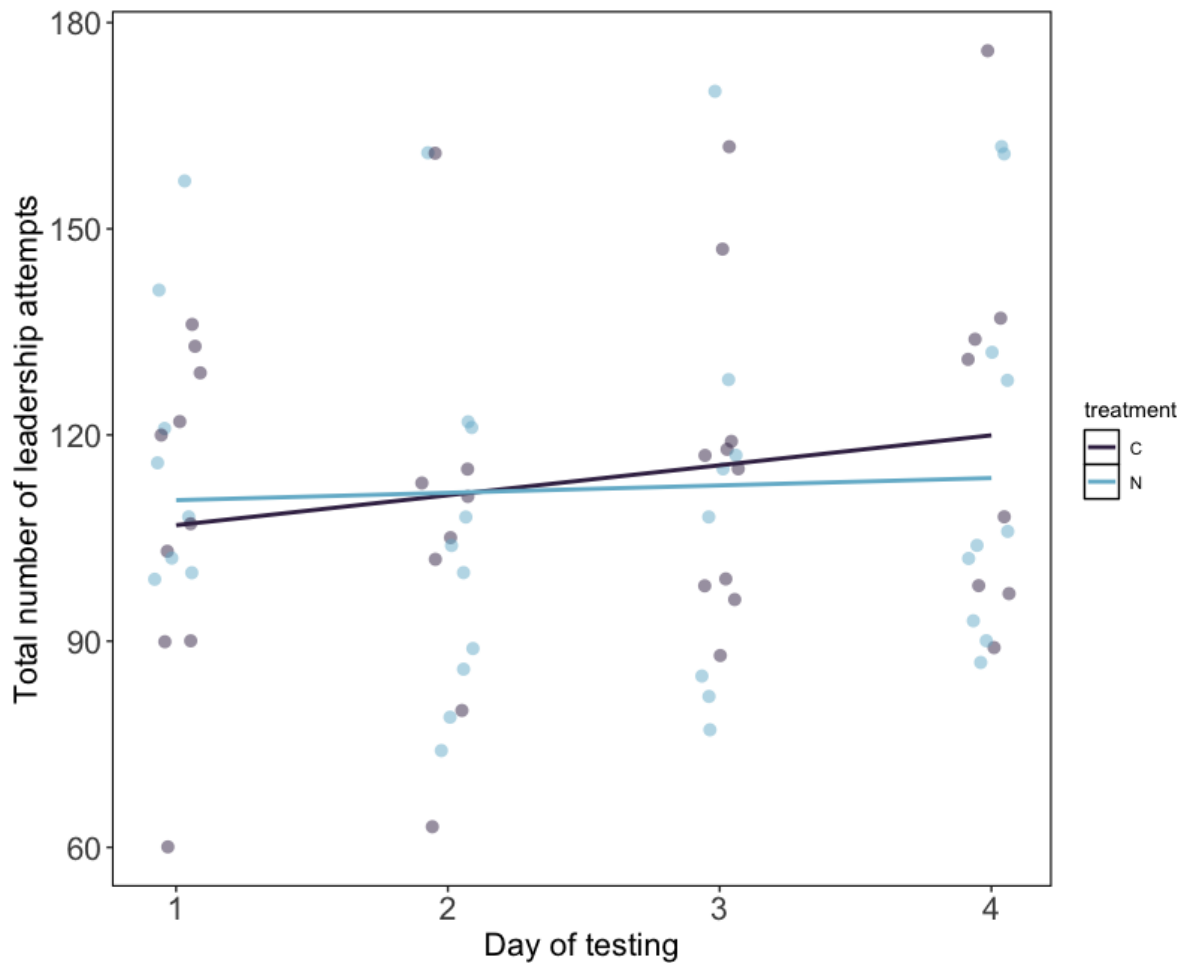


Figure 22. The relationship between the total number of leadership attempts and the day of testing in both noise and control treatments. Fitted lines are calculated from LMM fixed-effect estimates from the model with all main effects and the treatment * day interaction term. Points are individual data points (18 groups, 68 trials).

In models where the response variable was the number of following events, the best fitting model given the data was that with treatment and day as main effects only (Table 11). The next best model was that including day only ($\Delta\text{AICc} = 1.5$), followed by the model including the interaction term of treatment * day ($\Delta\text{AICc} = 1.9$). This suggests moderate-to-strong support for day and treatment to be the best predictors of the number of follower events, where removing treatment and including the interaction term do not improve the fit of the best model

(Table 7). The total number of following events increased over the days of testing, and is higher in the control treatment compared to the noise treatment (Figure 23).

Table 11. The ΔAICc for models explaining variation in the number of following events. Models differ in explanatory variables. The null model includes start time as the only fixed effect. All models include group identity as the random effect. Treatment is noise or control, day is the day of testing (1 – 4).

Explanatory variables	ΔAICc	d.f
Treatment + day + start time	0	6
Day + start time	1.5	5
Treatment * day + start time	1.9	7
Treatment + start time	7.4	5
Start time only (null model)	7.8	4

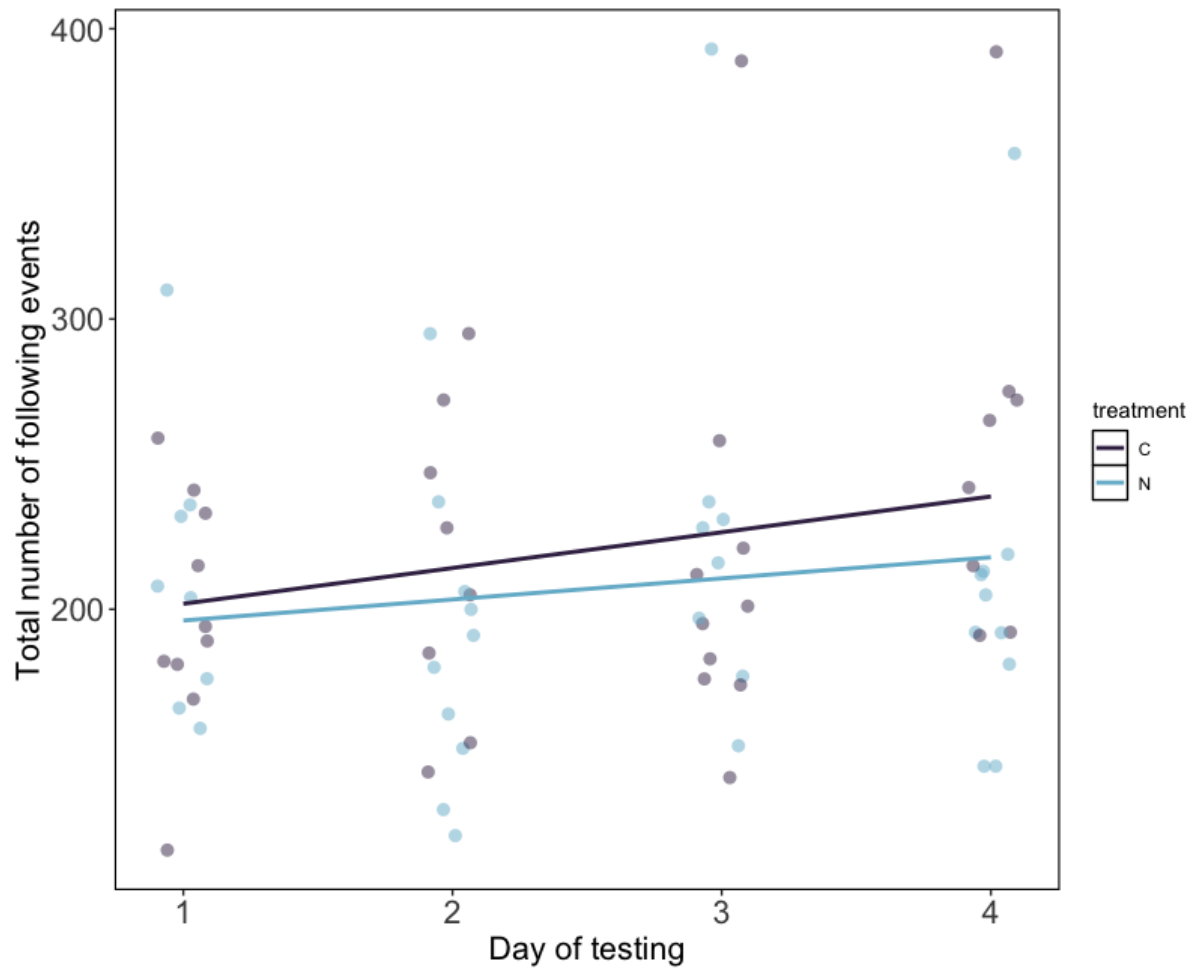


Figure 23. The relationship between the total number of following events and the day of testing in both noise and control treatments. Fitted lines are calculated from LMM fixed-effect from the model with all main effects and the treatment * day interaction term. Points are individual data points (18 groups, 68 trials).

Repeatability

For each response variable, comparing the model including all fixed effects with group identity to the same model lacking this random effect consistently found the models including the random effect had the best fit given the data (Table 12). All models with the random effect were greater than 2 AICc units less than the models without, demonstrating strong evidence

that there are consistent differences between groups that are not explained by any of the fixed effects (Figure 24).

Table 12. The ΔAIC_c for models with and without group identity as the random effect. Comparison shown for all response variables. Models contain the same fixed effects of start time, and the interaction between treatment (noise or control) and day of testing (1 – 4).

Response variable	Random effect	Model	ΔAIC_c	d.f
Mean speed of individuals	Group ID	Treatment * day + start time	0	7
	NA	Treatment * day + start time	35.8	6
Mean group cohesion	Group ID	Treatment * day + start time	0	7
	NA	Treatment * day + start time	8	6
Total moves into arms	Group ID	Treatment * day + start time	0	7
	NA	Treatment * day + start time	49.8	6
Ratio of leader to follower events	Group ID	Treatment * day + start time	0	6
	NA	Treatment * day + start time	26.6	5

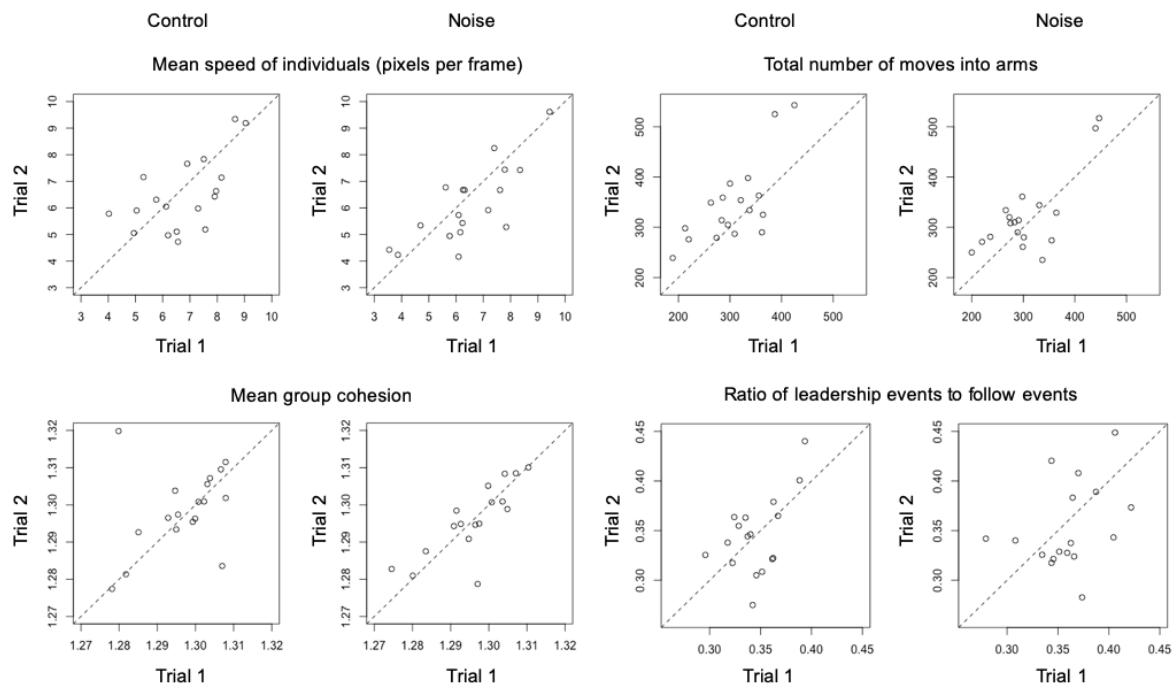


Figure 24. Relationships between response variables in the first and second control trials (left) and first and second treatment trials (right) for each response variable. Dotted line is $x = y$.

Discussion

The activity of groups changed over the days of testing, but not as a result of the treatment. Individuals swam more slowly over the testing period, being the fastest in the first trial. Conversely, the fish also became more exploratory, making more moves into the arms, over the days of testing. These results are likely related to the groups becoming habituated to the experimental arena over repeated testing, where they are more familiar with the tank, thus making more exploratory decisions. This result is supported by previous work on guppies habituating to stress exposure over repeated testing (Houslay *et al.*, 2019). However, it is interesting that where speed was higher movement between arms was lower. This could suggest guppies were swimming faster within arms on earlier days of testing. These responses did not appear to vary with the treatment; therefore, the addition of acoustic noise had no effect on activity or exploration within our experiment. This is in contrast to previous work, where swim speed increased as a result of acoustic noise (Currie *et al.*, 2020).

There was no change in group cohesion over the days of testing or as a result of treatment. This was unexpected, as previous studies demonstrate that anthropogenic noise can reduce cohesion and coordination in fish shoals of juvenile seabass (*Dicentrarchus labrax*; Herbert-Read *et al.*, 2017b) under laboratory conditions, and bluefin tuna (*Thunnus thynnus*; Sarà *et al.*, 2007) in the field. Conversely, Eurasia minnows (*Phoxinus phoxinus*) were found to be more cohesive when exposed to added continuous sound (Currie *et al.*, 2020). Our results found guppy shoal cohesion to be robust against the effects of added acoustic noise. However, these studies used recordings of anthropogenic noise sources rather than white noise, which may yield different responses as a result of stress (Voellmy *et al.*, 2014a). This is further supported by the fact these results are consistent with effects found in three-spined sticklebacks (*Gasterosteus aculeatus*), where the acoustic noise treatment was generated white noise (Ginnaw *et al.*, 2020).

In studies of collective movement, experiments often find that over repeated trials, group cohesion reduces due to habituation to experimental arenas (Miller and Gerlai, 2012; MacGregor and Ioannou, 2021). It is interesting this effect was not found with group cohesion, given that fish became less active and more exploratory, suggesting some level of habituation to the experimental tank.

The proportion of all moves that were leadership events was higher in the noise treatment than the control, with no change over the days of testing. Therefore, anthropogenic noise resulted in groups having relatively more leadership attempts versus control trials. Further analysis revealed that this was the result of there being fewer following events in the noise treatment compared to the control. There was no change in the number of leadership attempts as a result of treatment, demonstrating that individuals were not being more independent in the added noise treatment. From the data, it could not be determined whether more following events were a result of leadership attempts being less successful, i.e. a difference in the number of independent moves into arms that are followed by at least one fish, or whether it is a result of successful leadership attempts being followed by fewer fish when there was added noise.

Given our results for cohesion, this was not a result of groups being less cohesive overall. Added acoustic noise may be distracting individuals within a group from detecting social cues, likely caused by the distraction or stress effects of acoustic noise (Purser and Radford, 2011; Voellmy *et al.*, 2014a). These cues, such as the movements of other fish, are important for collective movement and decision-making (Ioannou *et al.*, 2011; Lemasson *et al.*, 2018). Our results suggest that noise could be restricting the ability of group members to use social information, and causing them to be unresponsive to leadership cues. This could have consequences for the fitness benefits provided by group-living, where the use of social

information is essential in allowing groups to make better decisions. From this study, we cannot determine whether these changes to group dynamics are disrupting social behaviour, or if these changes are an adaptive response to a change in conditions. Whether this change in following behaviour affects the performance of groups could be examined by testing the performance of groups in fitness related tasks, such as foraging or predator avoidance. Future experiments investigating this may yield further insights into the impact of noise pollution on collective decision-making.

Our results also showed there were consistent, repeatable differences in groups in all of our behavioural parameters, thus demonstrating group-level personality variation (Réale *et al.*, 2007; Bell *et al.*, 2009). These differences could not be explained by the day of testing or the experimental treatment. These results support previous work suggesting consistent among-group heterogeneity is widespread (Planas-Sitjà *et al.*, 2015; Salazar *et al.*, 2015; Jolles *et al.*, 2018; MacGregor and Ioannou, 2021). In this experiment, we were unable to track the identities of individuals within groups across the trials. Future work incorporating cross-trial individual identities into a similar experimental design could lend insights into how individual differences persist within groups that have consistent repeatable differences.

Our study provides novel insights into how acoustic noise impacts decision-making in fish shoals. While it could not be deciphered from our study whether these changes are adaptive or disruptive, i.e. whether they could have fitness consequences for groups, we have found that groups of guppies alter their following behaviour as a result of noise disturbance. Decision-making is a central component of collective behaviour, and disruptive changes in this could result in fitness consequences for individuals. Future study could consider this in different

contexts, with different noise sources, or assess the impact this has on the performance of groups and the outcomes of decisions.

Chapter 4

General Discussion

Overview

Social behaviour can be influenced by ecological contexts in numerous ways, due to behaviour itself being context dependant, and the degree to which individuals are sociable being a result of balancing the benefits and costs associated with group-living. In order to be maintained, group-living is mediated by social behaviours and environmental factors can reduce the ability of individuals and groups to perform these behaviours. Anthropogenic impacts leading to rapid change in environmental conditions can have consequences for the social interactions of animals, and thus group-living as a whole. In this thesis, I have examined how environmental change can impact sociability in fish shoals at two different scales. Firstly, developing a novel method for studying the aggregation and assortment of whole populations in the field. Here, I have considered natural environmental variation and infer social behaviour from distribution data. In contrast, my second study explored the impact of acoustic noise, a pollutant of increasing concern, on social behaviour at a fine scale. Under controlled laboratory conditions I was able to assess individual behaviour and group dynamics using digital tracking software. These two distinct approaches, while contrasting in their scale and approach, both provide novel insight into how social behaviour changes within different environmental contexts.

Summary of studies

In chapter 2, I found no effect of any of the recorded environmental variables on the aggregation of sticklebacks, in contrast to what has been previously found in laboratory studies of the same variables (Domenici *et al.*, 2002; Bartolini *et al.*, 2015; Chamberlain and Ioannou,

2019; Fisher *et al.*, 2021). Similarly, in chapter 3 I only found an effect of acoustic noise on the number of following events, and no impact on activity or shoal cohesion which was expected based on previous work (Herbert-Read *et al.*, 2017b; Sarà *et al.*, 2007).

My results in chapter 2 only show a trend for changes in sociability in the context of reproductive state, where during the breeding season sticklebacks were less aggregated.

This is likely due to increased aggressive interactions based on what is known about the life history traits of sticklebacks (Tinbergen, 1952; Huntingford, 1976; Kynard, 1978). This result provides evidence that individual state can influence social interactions between individuals, and that this can lead to changes in aggregation at the population level. The influence of reproductive state on sociability may further be exacerbated by environmental change. Breeding in sticklebacks is initially triggered by changes in temperature, and climate change can lead to warmer temperatures starting earlier in the year, and potentially lasting for longer. Changes in other environmental variables could also result in additional changes to aggression in sticklebacks, particularly if breeding occurs at a time of year where there are, for example, less resources (Fisher *et al.*, 2021). This could in turn reduce their sociability and tolerance for conspecifics (Fisher *et al.*, 2021). Fundamental understanding of how organisms and groups respond to ecological changes in natural conditions is essential for future work. Further, it is important to consider how the ecology and life history traits of a species may alter its response to the environment.

While these studies focus on different scales and stressors, a common theme in both was the tendency for study animals to habituate over experimental testing. Under laboratory conditions, this was found in parameters of activity and exploration. In the field, the result of less fish being caught over the weeks of data collection could be considered to be a result of habituation

over repeated testing, due to traps no longer appearing as a novel stimulus. However, in both of these cases habituation had no effect on social associations. Guppies under laboratory conditions did not become less cohesive, nor did sticklebacks in the field aggregate less, over repeated testing of the same individuals. This is again in contrast to previous work, where stickleback groups became less aggregated over repeated testing in laboratory experiments (MacGregor and Ioannou, 2021). Further, catching less individuals over the weeks of data collection could be a result of sticklebacks learning to avoid traps. In this case, it could be social learning, where in shoals individuals learn from other group-mates to avoid the opening of the trap (Lachlan *et al.*, 1998; Hoppitt and Laland, 2013). Alternatively, fish could be making decisions within a shoal to not enter traps, either through leadership or egalitarian processes.

Future directions

In the third chapter, I was able to closely assess fine scale interactions of individuals, and quantify specific behavioural parameters in a controlled environment. While this has revealed trends for how noise can affect social dynamics, these results cannot necessarily be extrapolated to the context of guppies in the natural environment or under anthropogenic noise pollution. Conversely, in the field I was able to assess dynamics under natural conditions, but lose the finer scale individual behaviours I could record in controlled laboratory trials. Further, it is harder to disentangle the impacts of different parameters in the field due to variation and correlations in environmental conditions. Using a combination of these approaches could allow investigation of social behaviour in natural conditions and at these disparate scales simultaneously. For example, combining the field study with GPS tracking of individuals in species that can be tagged would allow assessment of when and how individuals enter traps, or with underwater recordings where possible (Hughey *et al.*, 2018). Combing this method with

video data and tracking could also provide further information on whether fish enter traps as whole shoals or as a result of social attraction, and whether they learn to avoid traps over repeated testing.

While it is important to consider the effects of stressors in isolation, it is also important to keep in mind they are occurring simultaneously and result in multiple stressors (Orr *et al.*, 2020). Larger sample sizes in field studies, or the use of repeated measures designs with more than one type of treatment (e.g. Ginnaw *et al.*, 2020) could reveal more about how conditions and their impacts affect one another. Considering these combined effects will allow us to better understand dynamics under natural conditions (Ormerod *et al.*, 2010; Orr *et al.*, 2020).

Further to this, the effects of stressors will vary across taxa and ecosystems, thus it is hard to make broad conclusions about social behaviour under environmental change. Social network analysis could allow us to draw conclusions about social interactions across taxa in different environmental contexts by revealing patterns of change (Croft *et al.*, 2008; Wey *et al.*, 2008). This has previously been done for fish shoals with changes in habitat complexity (Webber and Haines, 2003; Orpwood *et al.*, 2008; Edenbrow *et al.*, 2011), and to assess ungulate herd dynamics with differences in resource availability (Rubenstein *et al.*, 2007; Sundaresan *et al.*, 2007; Williams *et al.*, 2017). Combining aspects of these studies could provide us with more knowledge on how to mitigate the potential effects of environmental stressors across ecosystems and species.

Conclusion

The results of these studies add to a growing body of research on how environmental conditions are altering the social behaviour of animals. Interestingly, my results are in some cases contrary to prediction and previous work. This highlights the need to consider the effects of environmental change in both natural settings and under highly controlled laboratory conditions. Social behaviours and group dynamics are crucial to the fitness of numerous species. Therefore, a greater understanding of how changes in the environment can influence the behaviours of individuals in a social context is essential in allowing us to mitigate the potential effects of anthropogenic stressors on global ecosystems.

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